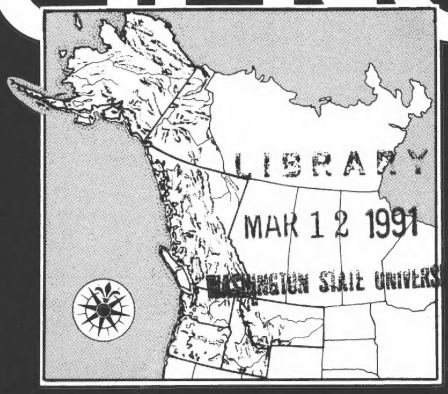
February 1991 Volume 65, Number 1

ANNUAL MEETING

NORTHWEST SCIENCE



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Reviewers of Manuscripts

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(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

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Announcements

Student Research Grants

Research grants in the amount of $300-500 will again be awarded to students. The successful recipients will be announced at the spring meeting of the Northwest Scientific Association. Short application forms can be obtained by writing to the Chairman of the Student Research Grants Committee. The completed forms should be returned no later than 15 March 1991. The short application form and further information can be obtained from:

Dr. Paul Doescher
Department of Rangeland Resources
Oregon State University
Corvallis, OR 97331

A Letter to the Members of Northwest Scientific Association

Dear Fellow Members:

On July 11, 1990 a strategic planning session was held at Washington State University-Vancouver to discuss proposals for changes in the nature and structure of NWSA and its journal. The participants represented a broad spectrum of interests and involvement within NWSA; a productive discussion of the mission and goals of NWSA was followed by recommendations for improvements to the organization.

The recommendations produced at the planning session were presented at the Fall 1990 Board of Trustees Meeting, and all recommendations were accepted for action by the Board. The most significant recommendation addresses the establishment of a position titled Executive Secretary for NWSA; a copy of the recommendation follows for your review. The membership will discuss and vote on this recommendation at the Spring 1991 Business Meeting.

The Board of Trustees encourages your participation in this action. Board members would be pleased to discuss this recommendation with you. We look forward to seeing you at the Annual Meeting of NWSA on March 20-22 at Boise State University in Boise, Idaho.

Respectfully,

Marcia Wicklow-Howard
President

Proposal for Executive Secretary

Mission Statement

The Northwest Scientific Association (NWSA) is organized to promote scientific inquiry and communication on subjects and issues of relevance to the Pacific Northwest. The organization encourages research and reporting, with the official publication of the NWSA, *Northwest Science*, disseminating information and improving the visibility of science in the Pacific Northwest. The NWSA promotes a scientific, interdisciplinary sense of community among scientists, and encourages the strengthening of interaction between the public and the scientific community by providing a credible source of scientific information. The Annual Meeting of NWSA and the journal, *Northwest Science*, facilitate communication among scientists, students, and the public in the Pacific Northwest.

Problem Statement

Continuity of Administration—The administrative structure of NWSA has the office of President rotating yearly. The appointment of President is often tied to the site of the Annual Meeting, and hence the individual holding the office may have limited experience in the organization and little knowledge of its goals. Given that the full responsibility for planning and hosting the annual meeting rests with this individual, many other responsibilities of the office may not be accomplished. Over time, this situation can lead to a serious lack in continuity in leadership and, subsequently, to a loss of organizational focus. Greater continuity in leadership and more communication throughout the administrative structure is necessary for the continued viability of NWSA.

Recommendation

The Governing Board of NWSA appoint a part-time *Executive Secretary* at a cost of up to $4,500.00/year for a trial period of two years.

The position of Executive Secretary would be set up as a two-year pilot project, with a probationary period of 90 days. Following review of the position in two years, the establishment of this position as a permanent part of the administrative structure would be put to a vote of the membership. The position is seen as one to assist with the details of running an organization, not a leadership role.

Functions of Executive Secretary

a. Assist with Journal—to facilitate communication between Governing Board and Journal Committee.
b. Record Keeping—to keep records on all awards, honors, scholarships awarded by NWSA; keep names and addresses of all recipients, and to generate appropriate correspondence; maintain updated Policy-By-Laws; and facilitate the adherence to NWSA policy.
c. Tracking Business—to follow up on discussions, recommendations, and responsibilities during the business year.
d. Business Calendaring—to aid in the development of the yearly calendar for all business meetings and functions associated with the Board.
e. Annual Meeting Coordination—to provide support to host institution with such things as mailing information, preparation of plaques for award recipients, and compilation of research grant applications.
f. Membership Lists—maintain up-dated list of members.
g. Budgeting—to assist with yearly budgeting for the administration of NWSA, and to provide assistance to institution hosting annual meetings.
h. Assist with ideas for promotion and marketing—to assist the Governing Board, Journal Editor, and institution hosting Annual Meetings with promotion of NWSA.

It is felt that the position of Executive Secretary will provide year-to-year continuity for the organization. This position can be funded at a cost of up to $4500.00/year *without* the need to increase membership dues. As a part of this recommendation is the suggestion that, although the term of office of the President will remain at one year, that the Past-President be appointed by the President as a member of the planning committee in order to add further continuity of administration.

Christopher J. Norment, Department of Zoology and Charles R. Conner Museum, Washington State University, Pullman, Washington 99164-4236[1]

Bird Use of Forest Patches in the Subalpine Forest-Alpine Tundra Ecotone of the Beartooth Mountains, Wyoming

Abstract

Relationships of bird species richness and abundance during the breeding season with forest area and edge were studied for ten forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. Species richness correlated equally well with area and edge, whereas mean number of individuals (abundance) correlated best with area. Among species that differed in their foraging habitats, species richness and abundance of those most restricted to foraging within forest habitat showed the best correlation with area. Species that foraged mostly in surrounding meadows and those that used both forest and meadow habitats correlated better with edge than with area.

Forest patches of intermediate size surrounded by meadow habitat had greater number of individuals per census than either smaller patches or a larger plot within a continuous forest stand. Number of species in intermediate-sized patches was greater in smaller patches, and approximately equal to that in the continuous forest stand. These results are attributed to the combined presence of edge habitat from which birds may forage into surrounding meadow and sufficient forest habitat for those species restricted to foraging within forest. Patterns of species distribution, importance of edge, and changes in avian community composition across the range of forest patches studied tentatively suggest that some predictions developed from the study of bird communities in forest fragments created by human disturbance may not be applicable to communities in naturally occurring forest patches in western montane coniferous forests.

Introduction

Many studies have shown that number of bird species and individuals using small patches of woodland increase with area, both where forest fragmentation has resulted from human activity (Galli *et al.* 1976, Whitcomb *et al.* 1981, Howe 1984, Hayden *et al.* 1985, Temple 1986, Blake and Karr 1987), and where woodlots have been planted in a surrounding matrix of croplands (Martin 1981a). These results have generated concern that continued loss and fragmentation of forest habitat will cause long-term declines in some forest bird populations (Robbins 1979, Butcher *et al.* 1981, Whitcomb *et al.* 1981, Ambuel and Temple 1983, Blake and Karr 1987).

Given current interest in the effects of habitat destruction on the decline of temperate forest breeding birds, examination of bird communities in naturally-occurring forest patches is important because these communities presumably are no longer adjusting to processes of habitat fragmentation (see Rosenberg and Raphael 1986). I analyzed the relationship between bird species richness and number of individuals (hereafter referred to as abundance) and area of small forest patches in a forest-tundra ecotone, and tested the prediction that species most dependent upon forest vegetation will show the greatest response to differences in forest area. To my knowledge, a study of this nature has not been previously undertaken in a habitat unaffected by human activity.

Methods

I studied bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. The ecotone is a mosaic of plant communities resembling those of the continuous subalpine forest or alpine tundra in physiognomy and taxonomic composition. Discrete forest stands within the ecotone occur on rocky, well-drained sites and are surrounded by meadow vegetation. There is a sharp transition between the two plant communities. Many stands occur on outcrops of rocky, well-drained soil, and are roughly circular in shape; others are narrow (ca. 20 to 50 m) strips of "ribbon forest" between broad bands of subalpine meadow, and probably have resulted from a combination of strong winter winds, snowdrift accumulation patterns, and cool summers (Billings 1969).

Ten study sites were selected to minimize differences in habitat variables other than area and edge. All sites were between 2900 and 2960 m^2 elevation and 25 to 100 m from adjacent stands of trees. All forest patches contained Englemann spruce (*Picea englemannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*).

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TABLE 1. Characteristics of the ten forest patches, 1980 and 1981.

Site #		Area (m^2)	Edge (m)	Number of censuses (n)	Species richness	Mean species/ census ($\bar{x}$ ± SD)	Mean individuals/ census ($\bar{x}$ ± SD)
1980	1	600	90	5	3	0.6 ± 0.5f	0.4 ± 0.5
	2	1,200	140	5	6	3.2 ± 1.6	3.0 ± 2.4
	3	2,000	170	5	6	1.6 ± 1.1	2.8 ± 2.6
	4	5,900	330	5	5	2.2 ± 1.3	3.4 ± 3.1
	5	6,200	450	5	10	3.3 ± 0.5	5.4 ± 1.3
	6	9,000	400	5	11	5.2 ± 0.8	10.2 ± 4.0
	7	19,000	750	5	12	6.1 ± 1.1	13.0 ± 9.3
	8	22,000	580	5	13	7.4 ± 2.3	12.8 ± 6.0
	9	23,000	600	5	9	5.6 ± 1.7	14.6 ± 6.0
	10	40,000	0	5	10	5.8 ± 0.5	11.6 ± 3.6
1981	5	6,200	450	11	10	4.0 ± 1.0	7.1 ± 3.5
	7	19,000	750	11	15	7.6 ± 2.1	17.0 ± 5.8
	8	22,000	580	8	15	7.6 ± 1.6	13.6 ± 4.3
	10	40,000	0	11	15	7.0 ± 1.4	14.7 ± 4.9

Average canopy height was about 8 m. Understory vegetation was sparse, consisting primarily of whortleberry (*Vaccinium scoparium*).

Nine patches surrounded by meadow habitat varied in area from 600 to 23,000 m^2 (Table 1). To compare bird abundance in patches relative to a larger, non-isolated stand, an additional plot of 40,000 m^2 was established in a continuous forest stand of ca. 6 ha. Because I wished to analyze how reduced edge affects richness and abundance of forest interior species, boundaries were placed as far from the nearest forest/meadow habitat discontinuity as possible. Boundaries were ca. 50 m from the nearest meadow on three sides of the plot, and 25 m from meadow on the other, although some edge impacts may extend further into deciduous forest fragments (Temple 1986). Size of the plot, and distance of boundaries from the nearest meadow habitat, were limited by the discontinuous tree distribution in the ecotone.

Forest patches were mapped in the field with a 50-m tape and hand-held compass. Area of each patch was calculated by cutting out each forest patch from a map of the study area, weighing it to the nearest 0.001 g on an analytical balance, and dividing the weight by weight per unit area. Perimeter of each forest patch, hereafter referred to as "edge," was determined directly from field measurements using a 50-m tape.

Each site was censused five times during the breeding season in 1980. For comparative purposes, four plots were censused at least eight times in 1981. During each visit, I walked slowly through the site and recorded all individuals seen or heard. A minimum of 15 min/census was allocated to the smallest patches, and no census lasted more than 1.5 h. A 25 m × 25 m grid was established in the largest plot to facilitate census work. Most censuses were conducted between 0600 and 1030; each stand was also censused at least once between 1900 and 2100 to hear evening thrush choruses.

During census work in forest plots and surrounding meadows, I quantified avian habitat choice (either meadow or forest) for actively foraging birds. Data were recorded at 15-s intervals signaled with a tone pulse emitted by an electronic metronome (Wiens *et al.* 1970). No more than five observations were recorded on a single bird to reduce sampling bias. Although sequential observations of individual birds are not independent (Morrison 1984), I wished to follow each bird through a series of foraging activities and not bias my data towards conspicuous birds by recording a single observation of each bird encountered (see Wagner 1981). Species represented by fewer than 30 observations were classified according to accounts in the literature. Three foraging habitat groups (FHGs) were recognized (Table 2): 1) species for which ≥ 90 percent of all foraging observations were in meadow habitat; 2) species for which ≥ 90 percent of all foraging observations

TABLE 2. Mean abundance (number of individuals/census/plot) and foraging habits of bird species in small forest patches (600-6,200 m²), medium forest patches (9,000-23,000 m²), and a large continuous forest tract (40,000 m²). Values are averaged for all censuses, 1980 and 1981. Number of plots in each size class are given in ( ).

Species	Abundance (individuals/census/plot)			Foraging habitat				
	Small patches (n=5)	Medium patches (n=4)	Continuous tract (n=1)	FHG[1]	n	% Meadow	% Forest	Ref.[2]
Hairy Woodpecker (*Picoides villosus*)	0	0.03	0	F	4	0.0	100.0	1,9
Northern Flicker (*Colaptes auratus*)*	0.04	0.04	0	G	6	100.0	0.0	1,7
Gray Jay (*Perisoreus canadensis*)*	0.05	0.13	0.94	F	7	0.0	100.0	2
Clark's Nutcracker (*Nucifraga columbiana*)#	0.22	1.39	1.06	G	14	57.1	42.9	2,10
Mountain Chickadee (*Parus gambeli*)*	0.16	1.00	1.50	F	96	0.0	100.0	
Red-breasted Nuthatch (*Sitta canadensis*)#	0	0.03	0.19	F	9	0.0	100.0	3,9
White-breasted Nuthatch (*Sitta carolinensis*)*	0	0.10	0.06	F	0			3,9
Ruby-crowned Kinglet (*Regulus calendula*)*	0	0.81	1.19	F	37	0.0	100.0	
Mountain Bluebird (*Sialia currucoides*)*	0.31	0.74	0.06	M	161	93.2	6.8	
Hermit Thrush (*Catharus guttatus*)#	0	0.02	0.13	F	0			4
American Robin (*Turdus migratorius*)*	0.84	2.60	1.44	M	82	93.9	6.1	
Water Pipit (*Anthus spinoletta*)	0.72	0.29	0	M	178	100.0	0.0	
Yellow-rumped Warbler (*Dendroica coronata*)*	0.21	0.77	1.13	F	54	0.0	100.0	
Chipping Sparrow (*Spizella passerina*)*	0	0.21	0.06	G	30	60.0	40.0	
Vesper Sparrow (*Pooecetes gramineus*)	0.04	0	0	M	4	100.0	0.0	5
White-crowned Sparrow (*Zonotrichia leucophrys*)*	1.12	1.48	0	G	147	68.1	31.9	
Dark-eyed Junco (*Junco hyemalis*)*	0.68	2.44	3.44	G	116	37.9	62.1	
Rosy Finch (*Leucosticte arctoa*)	0	0.02	0	M	51	100.0	0.0	
Cassin's Finch (*Carpodacus cassinii*)*	0.29	1.48	0.09	G	78	57.8	42.2	
Pine Grosbeak (*Pinicola enucleator*)*	0.08	0.28	0.94	G	24	20.8	79.2	5,6,8
White-winged Crossbill (*Loxia leucoptera*)	0	0	0.13	F	2	0.0	100.0	5
Pine Siskin (*Carduelis pinus*)#	0	0.11	0.75	G	15	33.3	66.7	5,8

[1]FHG = Foraging habitat group; M = meadow-foraging species, G = generalists, F = forest-foraging species.

n = number of foraging observations.

[2]Ref = references on foraging; 1 = Bent 1939; 2 = Bent 1946; 3 = Bent 1948; 4 = Bent 1949; 5 = Bent 1968; 6 = French 1954; 7 = Gabrielson and Jewett 1940; 8 = Newton 1972; 9 = Stallcup 1968; 10 = Tomback 1977.

*Species known to breed within forest stands in the ecotone.

#Species that probably breeds within forest stands in the ecotone.

were in forest habitat; and 3) generalists that foraged in both forest and meadow habitats.

I examined species-area, abundance-area, species-edge, and abundance-edge relationships using log-log (power), semi-log (exponential), and untransformed (linear) regression functions (Martin 1981a). Best-fit functions were determined by comparisons of correlation coefficients; I determined significance of the coefficients with tables in Rohlf and Sokal (1981). Relationships of FHGs to area and edge were also examined with regression functions. Additionally, proportion of the total avian community comprised by each FHG was compared among three plot size classes: small tracts from 600 to 6,200 m^2 (n=5); medium tracts from 9,000 to 23,000 m^2 (n=4); and the largest tract (40,000 m^2). Proportion of species and total individuals in the three FHGs were calculated for each patch, based on cumulative data from all censuses. Proportions were then averaged over all plots in each size class. Size classes were separated between 6200 and 9,000 m^2 to include approximately equal numbers of patches in the small and medium classes.

Results

Species Richness and Abundance

Species richness for the nine smaller forest patches increased with both area ($Log_eY = 0.474 + 0.323Log_eX$; $r = 0.860$, $P < 0.01$) and edge ($Log_eY = 0.305 + 0.561Log_eX$; $r = 0.863$, $P < 0.01$) in 1980, with power functions providing the best fit (Fig. 1). Mean number of species per census did not differ for plots censused in both years (t-tests, $P > 0.10$). Mean abundance (individuals per census) also increased with both area ($r = 0.914$, $P < 0.01$) and edge ($r = 0.863$, $P < 0.01$) in 1980, with the linear function providing the best fit (Fig. 1). There were no between-year differences in mean abundance for patches censused in both 1980 and 1981 (t-tests, $P > 0.10$).

Several results indicate that species richness and abundance were lower in the largest forest plot, which lacked adjacent meadow habitat, than in intermediate-sized forest patches surrounded by meadow. First, at least as many individuals and species were observed per census in intermediate patches as in the largest plot, despite an approximately 200 percent difference in area (Table 1). The species richness curve also appeared to level off at an asymptote above 22,000 m^2 (Fig. 1). Second, bird abundance in the largest plot fell below

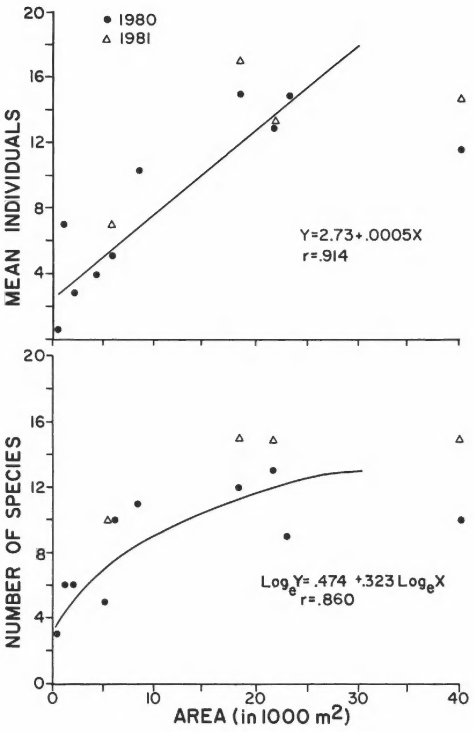

Figure 1. Mean number of individuals per census (top) and total number of bird species (bottom) plotted against area for the nine smaller forest patches. Regression lines are based upon 1980 data only (closed circles); data for 1981 (open triangles) and largest patch (plot without edge) are shown for comparison.

values predicted by the regression equation calculated from data for the nine smaller patches (Fig. 1).

Foraging Habitat Groups

Of the 22 species observed, eight were placed in the generalist FHG, five in the meadow FHG, and nine in the forest FHG (Table 2). The meadow FHG included species that used forest patches for nesting [American Robin and Mountain Bluebird (all scientific names are given in Table 2)] and perch sites only (Water Pipit, Rosy Finch, and Vesper Sparrow). Except for the Dark-eyed Junco, generalists usually nested in forest habitat, although White-crowned Sparrows also nested under willow (*Salix*) clumps in meadows. Based on foraging observations and literature references (see Table 2), I placed several species that feed primarily on

seeds, buds, or foliage during much of the year in the generalist FHG (Clark's Nutcracker, Pine Grosbeak, and Pine Siskin).

FHG Distribution Patterns

As predicted, meadow species were not correlated with forest patch area ($r = 0.566$, $P > 0.05$), while number of generalist species ($r = 0.893$, $P < 0.01$) and forest species ($r = 0.773$, $P < 0.05$) increased with forest patch area. When data from the largest plot were added to the regressions, the fit was decreased for meadow species and generalists, and increased ($r = 0.843$) for forest species. Edge was a better predictor of species number for the meadow FHG in forest patches ($r = 0.678$, $P < 0.05$), even though robins and Mountain Bluebirds nested within the forest patches and up to 50m from the forest edge. Edge was also a better predictor of species richness for generalists ($r = 0.911$, $P < 0.01$).

Regression of mean abundance per census against area, based on data for the nine smallest plots, were significant for the generalist ($r = 0.945$, $P < 0.01$) and forest ($r = 0.839$, $P < 0.01$) FHGs. When data from the largest plot were added, a better fit was provided only for the forest FHG ($r = 0.912$). Removal of generalist FHG species that presumably relied more heavily on resources within forest patches than in surrounding meadows (Pine Grosbeak, Clark's Nutcracker, and Pine Siskin) from the abundance-area regression reduced the fit to $r = 0.680$ for the generalist FHG. As with species number, edge provided the best estimate of abundance ($r = 0.678$, $p < 0.05$) for the meadow FHG.

As plot size increased, forest species and individuals represented an increasing proportion of the total community (Fig. 2). Proportions of generalist species and individuals were similar in all plot sizes. Meadow FHG species and individuals represented a larger proportion of the community in small patches than in intermediate patches or the largest plot.

The meadow-foraging American Robin and the generalist Dark-eyed Junco, which foraged primarily on the forest floor and in small clearings (Norment, unpublished data), were the only species abundant on all plots (Table 2). Only meadow and generalist species were observed at rates ≥ 0.5 individuals per census in small patches. Included in this group were Dark-eyed Juncos, Water Pipits,

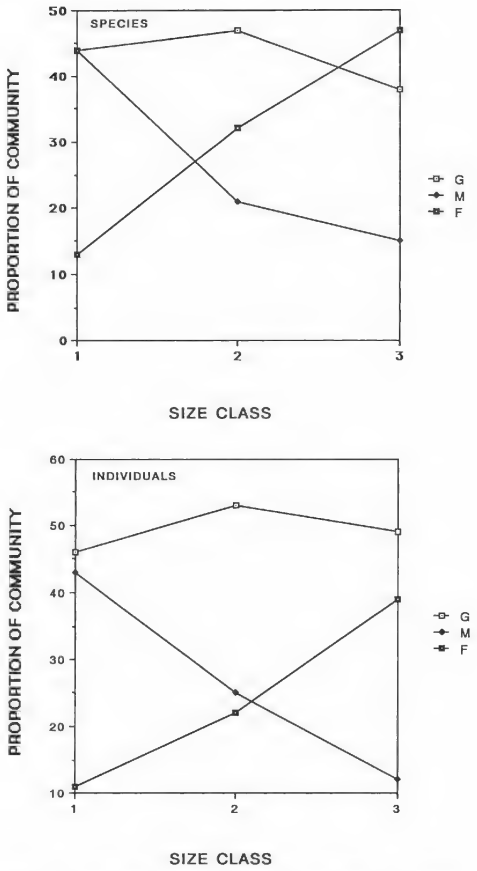

Figure 2. Average percent of total observations (number/census/plot) of species (top) and individuals (bottom) contributed by the forest FHG (F), generalist FHG (G), and meadow FHG (M) in the three plot size classes (1 = 600-6,200 m^2; 2 = 9,000-23,000 m^2; 3 = 40,000 m^2).

White-crowned Sparrows, and American Robins; the two latter species nested in very small forest patches (≤ 100 m^2) in other parts of the ecotone. Many generalist and meadow species were restricted to forest habitat near the periphery of patches, and were rarely, if ever, observed in the largest plot, which had boundaries ≥ 25 m of the nearest meadow habitat. Included in this group were the Northern Flicker, Mountain Bluebird, Water Pipit, Cassin's Finch, Chipping Sparrow, and White-crowned Sparrow (Table 2).

Members of the forest FHG were abundant only in forest patches $\geq 9{,}000$ m^2 (Table 2). The only

common members of the foliage-gleaning guild—Mountain Chickadee, Ruby-crowned Kinglet, and Yellow-rumped Warbler—were most frequently encountered in the largest plot. Bark probers and gleaners (e.g., Hairy Woodpecker and Red- and White-breasted Nuthatches) were rarely observed in the subalpine forest-alpine tundra ecotone.

Discussion

The current study is similar to previous studies of bird communities in forest fragments in that increased area accounted for increased species richness and abundance (Galli *et al.* 1976, Ambuel and Temple 1983, Freemark and Merriam 1986, Temple 1986, Blake and Karr 1987, and others). However, the strong response of the meadow and generalist FHGs to edge suggest that it is also important in determining bird species richness and abundance in forest patches in the Beartooth Mountains. Forest patch area appeared to be more important than edge for species that rely on forest habitat for both nesting and foraging.

Relatively few studies have directly analyzed edge as a variable influencing bird communities in woodland fragments. Bird species richness and abundance in South Dakota shelterbelts were positively, but less strongly, correlated with edge than with area (Martin 1981a), although the converse was found for bird communities in Minnesota shelterbelts (Yahner 1983). Bird species richness also was positively correlated with plot edge in Douglas-fir (*Pseudotsuga menziesii*) forests in California (Rosenberg and Raphael 1986). Bird species richness in Illinois forest fragments correlated most strongly with area, although some species were also influenced by amount of woodlot edge (Blake and Karr 1987).

Ecological generalists that feed in both forests and surrounding habitats are important components of bird communities in many forest fragments (Galli *et al.* 1976, Martin 1981a, Whitcomb *et al.* 1981, Blake 1983, Hansson 1983, Howe 1984, Hayden *et al.* 1985, Haila 1988). In the Beartooth Mountains, intermediate-sized patches may support more birds than either small patches or the interior areas of continuous forest because they contain sufficient habitat for forest species and are surrounded by meadows that provide abundant food for species nesting in forest stands. Use of surrounding habitat for foraging may account for increased nesting densities in riparian communities and shelterbelts surrounded by agricultural fields that provide abundant resources but lack suitable nest sites (Carothers *et al.* 1974, Martin 1981a).

Absence of species that require edge or nearby meadow habitat may partially explain lower abundance and lack of increase in species richness in the continuous forest plot. However, three additional factors may also be important. First, the largest plot may have been too small to attract forest interior species that require extensive blocks of habitat. The number of species present on the largest plot, and which probably bred in forest stands in the ecotone (15), was less than the number of breeding season non-raptors in larger areas in two other northern Rocky Mountain spruce-fir forests (Salt 1957, Thompson 1978). This could explain the absence from the ecotone of six species reported in each of the above studies, and two guilds generally present in Rocky Mountain spruce-fir forests: timber-drill, and air-perch-soar (see Smith 1980). A similar explanation may account for the absence of woodpeckers from small, forested lake islands (Howe 1979). However, potential area effects are the result of limitations on the avian community caused by patchy tree distribution and limited stand size in the ecotone, rather than arbitrary use of small plots. Whether larger plots would have yielded greater numbers of species and individuals is, in some ways, a moot point since larger, continuous stands were not found.

Second, relatively few neotropical migrants, such as wood warblers (*Dendroica* spp.) nest in spruce-fir forests (Smith 1980). Neotropical migrants are strongly affected by forest fragmentation and their species richness and abundance show strong area-dependent responses (Lynch and Whitcomb 1978, Keast and Morton 1980, Whitcomb *et al.* 1981).

Third, Englemann spruce comprised 70 percent of the trees in forest patches in the ecotone (Norment, unpublished data). Englemann spruce forests support poor avifaunas, particularly of foliage-gleaning species (Smith 1980), and bird species richness and densities decrease as Englemann spruce increases in abundance (Austin and Perry 1979, Smith and MacMahon 1981). Low densities may be due in part to low abundances of ground and foliage arthropods (Fichter 1939, Hayward 1945, Norment, unpublished data).

Conversely, forest birds capable of foraging in meadows in the Beartooth Mountains can exploit abundant arthropod populations during much of their breeding cycle (Norment 1987). Whatever the ultimate cause, a small source pool, or high ratio between number of species present in a series of habitat patches or islands and source pool size, should decrease the strength of the area response in island (or patch) situations (Schoener 1976, Martin 1981b). Thus the combined effects of a small source pool of spruce-fir forest interior species, small forest patch size, low resource levels, and lack of edge habitat may explain the relatively low bird abundance and lack of increase in species richness in the continuous plot.

Because the study did not include replicates in the largest size class, differences between the continuous forest plot and smaller forest patches could be due to specific site characteristics and not to more general effects related to area. However, census data from forest interiors ($\geq$ 25 m from the nearest edge) throughout the ecotone collected during 1980, 1981, 1984, and 1987 (Norment, unpublished data) suggest that this habitat is generally depauperate in bird species and individuals. Only 15 species were observed to nest in forest interior habitat, and all of these except the Hairy Woodpecker were observed in the large plot (Table 2). Additionally, cumulative detection rates (number of individuals observed/hour) in the interior of six forest patches $\geq$ 2.0 ha were very low or 0 for species rarely seen in the large plot. For example, cumulative detection rates for the Northern Flicker, Mountain Bluebird, Cassin's Finch, and White-crowned Sparrow were 0.07, 0.05, 0.16, and 0.05 individuals/hr (Norment, unpublished data).

Responses of bird communities to differences in area of forest fragments are influenced by patterns of resource distribution, habitat heterogeneity, the surrounding habitat matrix, isolation of forest patches, composition of the species source pool, and time since fragmentation (Butcher *et al.* 1981, Martin 1981a, Whitcomb *et al.* 1981, Blake 1983, Howe 1984, Freemark and Merriam 1986, Rosenberg and Raphael 1986, Blake and Karr 1987). Because physical and biotic characteristics of western montane coniferous forests and eastern deciduous forests differ, responses to habitat fragmentation by bird communities in these forest types also may be expected to differ (Reese and Ratti 1988). At higher elevations in the Beartooth Mountains, forest bird communities may respond less strongly to area than forest bird communities in eastern and midwestern forest fragments, although this conclusion would be strengthened by further comparative work in forest patches and continuous forest. Presumably, a long-lasting equilibrium exists between meadow and forest vegetation in the Beartooth Mountains (Billings 1969), and forest bird communities are not presently adjusting to habitat changes. Instead, abundant resources in surrounding meadows, the presence of relatively few species strongly affected by habitat fragmentation, and the highly fragmented nature of the forest-tundra ecotone may produce a system in which intermediate-sized forest patches contain more individuals than larger patches, and edge is a better predictor of species richness than area.

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Understory Vegetation Response to Increasing Water and Nitrogen Levels in a *Pinus ponderosa* Forest in Northeastern Oregon

Abstract

Competition for soil moisture has been proposed as the dominant environmental resource governing understory production in pine forests of eastern Oregon. Other studies have demonstrated that light and nitrogen may also be limiting understory growth. The objective of this research was to test the hypotheses that both water and nitrogen and/or their interaction limit understory biomass production in a *Pinus ponderosa* (ponderosa pine) forest in northeastern Oregon. The experiment was a completely randomized block design with three blocks and four treatments: 1) control, 2) water (irrigated biweekly), 3) nitrogen (NH_4 NO_3, 32 percent N; 50 kg N ha^{-1}), and 4) water + nitrogen. At peak standing crop (June 26 through July 7) the water + nitrogen treatment produced 16 and 18 percent greater aboveground dry weight biomass than the nitrogen and water treatments and 36 percent more than the control treatments. Nitrogen and water treatments were 17 and 15 percent more productive than the control treatment. There was no relationship between light (PAR), measured at the center of each plot with light sensitive ozalid paper, and biomass production. Understory vegetation is significantly limited by both water and nitrogen in *P. ponderosa* forests of northeastern Oregon.

Introduction

Competition for limited resources, such as light, water, and nutrients governs forest understory vegetation production. Light is often the limiting environmental variable controlling understory plant communities in mesic forests (Christy 1986). Water or competition for soil moisture has been proposed as the dominant environmental factor governing understory production in more xeric pine forests in eastern Oregon (Krueger 1980). In a previous study we investigated the effect of resource limitation on understory growth in a *Pinus ponderosa* forest in northeastern Oregon (Riegel 1989). Competition for resources was separated into above ground and below ground components by commercially thinning to increase light to the understory and by trenching the perimeters of plots to sever tree roots growing inside. Understory biomass significantly increased when overstory root competition was reduced for belowground resources, regardless of light levels on the plot. We were uncertain, however, if understory growth increased due to increased levels of soil moisture, nutrients, or a synergistic effect.

The concept of resource limitation was developed in agriculture to refer to the limitation of productivity (Chapin 1980, Chapin *et al.* 1986). The more resource-limited an individual or community is, the more its production increases in response to an addition of the limiting resource. This relationship between resource availability and productivity provides objective criterion for evaluating the extent of resource limitation to the production of individual plants or a community. If specific resources are limiting, their addition will increase productivity.

We designed an experiment to test the effect of increasing limited resources, soil moisture and nitrogen, on understory vegetation biomass production in a *P. ponderosa* forest in northeastern Oregon. Our objectives were to test the hypotheses that both water and nitrogen and/or their interaction limit understory biomass production in this ecosystem.

Study Area

The study was conducted on the Hall Ranch of the Eastern Oregon Agricultural Research Center, located approximately 19 km southeast of Union, Oregon (Figure 1). The Hall Ranch is within the southwestern foothills of the Wallowa Mountains in the northeastern corner of the state at an elevation of approximately 1060 m.

The climate is continental with cold wet winters, and hot dry summers with occasional thunderstorms. Mean monthly air temperature extremes vary from a minimum of −19.2°C in December

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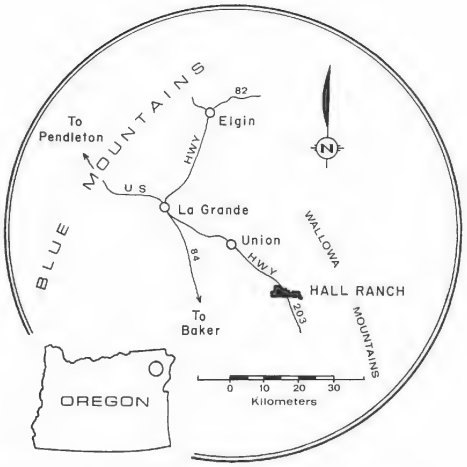

Figure 1. The Hall Ranch, location of the study area.

to 1.1°C in July; from a maximum of 8.5°C in December to 36.9°C in July (file data; Eastern Oregon Agricultural Research Center, Union). The majority of precipitation on the Hall Ranch occurs between November and June in the form of snow during the winter. Mean annual precipitation for 1963-1987 was 605 mm (Williams 1988).

The experiment was conducted in a *Pinus ponderosa/Symphoricarpos albus* (white snowberry) community type similar to Johnson and Simon's (1987) *Pseudotsuga menziesii* (Douglas-fir)/*Symphoricarpos albus* plant association of the Wallowa-Snake Province of northeastern Oregon. *Pinus* dominates the overstory and codominates reproduction with *Pseudotsuga menziesii.* Density of the overstory was 345 trees ha^{-1}, basal area 22 m^2 ha^{-1}, and tree diameters at breast height (dbh) ranged from 0.3 to 135.6 cm with a mean of 31.8 cm. *Symphoricarpos, Carex geyeri* (elk sedge), *Calamagrostis rubescens* (pinegrass), and *Arnica cordifolia* (heartleaf arnica) dominate the understory. Sites were selectively logged before 1936; since then there has been no logging.

Three major soil series occur within the research site: the Hall Ranch series, fine-loamy, mixed, frigid, Ultic Haploxerolls (block 1 non-thin and thin; block 2 thin); the Klicker series, loamy skeletal, mixed frigid Ultic Agrixerolls (blocks 2 and 3 non-thin); and the Tolo series, medial over loamy, mixed frigid Typic Vitrandepts (block 3 thin) (Dyksterhuis and High 1985). Surface soil texture ranges from silt loam to silty clay loam and soil depth varies from 38 to greater than 92 cm.

Methods

On April 15, 1987, 120, 1 x 1 m plots were established in the understory of a *Pinus* forest. The experiment was a completely randomized block design. Three 5.0 ha stands or blocks were selected for this study. Stands were considered to be relatively homogeneous in species composition and stand structure, however, understory species composition varied slightly among blocks. Four treatments: 1) control, 2) water, 3) nitrogen, and 4) water + nitrogen were randomly assigned to each plot by block. There were 10 plots per treatment within each of the three blocks.

Nitrogen (NH_4, NO_3, 32 percent N) was applied by hand at 50 kg N ha^{-1} on each nitrogen plot on April 15th, prior to spring growth. The amount of nitrogen applied to the forest floor was supplemented to approximate mineralization of tree roots and subsequent fertilization response in trenched plots, where tree root competition was removed, from our earlier study (Riegel 1989). We calculated the additional nitrogen requirement by taking the 1986 biomass production from the non-thinned/trenched plots, 1711.99 kg ha^{-1} x 1.5 percent nitrogen in plant tissue (Marschner 1986) = 25.68 kg ha^{-1}, then doubled that value to insure a response (Timothy L. Righetti, personal communication). Approximately 85.02 mm of precipitation (John D. Williams, personal communication) was received from the date of fertilization through the last day biomass was harvested (July 7).

Water treatments were irrigated biweekly from May 6 through June 18 to simulate the increase in soil water after tree roots growing in trenched plots had been severed (Riegel 1989). Our objective was to ameliorate the amount of soil water the understory received after tree root competition had been reduced after trenching, a difference of 10-15 percent between trenched and non-trenched treatments. The amount of water required to simulate higher soil water content was calculated for a soil volume of 100 x 100 x 50 cm (depth) = 500,000 cm^3. To increase soil water by 10 percent in the 0-20 cm depth, we measured bulk density 0.9 gm/cm^3 x 500,000 cm^3 = 45,000 gm soil, which is approximately 22.5 L of water, assuming 50 percent porosity. As the season progressed we increased the amount of water to 30 L on May 21,

and 40 L June 3 and 18. Soil moisture was measured gravimetrically at three depths (0-20, 20-40, and 40-60 cm) both inside and adjacent to each plot 24 hours after watering on May 21 and June 4. To construct the soil water release curves, gravimetric soil moisture was converted to volumetric soil moisture content. A representative soil water release curve for the 0-20 cm depth is shown in Figure 2. Soil water retentivity was determined on a pressure plate membrane apparatus (Soil Physics Laboratory, Soil Science Department, Oregon State Univ., Corvallis).

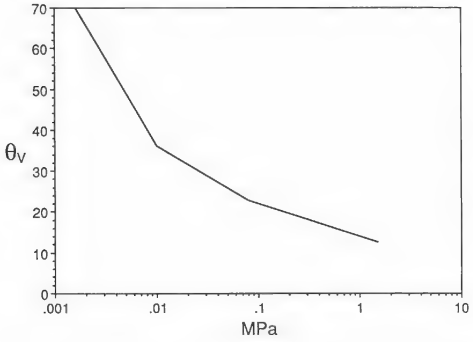

Figure 2. Representative soil water release curve of the 0-20 cm depth from block 1, the Hall Ranch soil series. The x axis is soil water potential (MPa) and the y axis, percent volumetric soil moisture (Θ_v).

Plots were clipped at peak standing crop beginning June 26 through July 7. Immediately prior to clipping, each plot was photographed to assist with interpreting results. *Carex* was clipped and bagged separately. Biomass was dried for 48 hours at 60°C and weighed.

Carex biomass samples were pooled by treatment within blocks for nitrogen analysis. Nitrogen concentration was determined with a semimicro-Kjeldahl apparatus (Bremner 1965). Nitrogen total accumulation of biomass is defined as the total quantity of nitrogen in the above ground portion of the plant per unit area (kg ha^{-1}), derived by multiplying the nitrogen concentration of *Carex* x total biomass (kg ha^{-1}) of each plot (Jarrell and Beverly 1981).

Light, photosynthetic active radiation (PAR), was quantified for each plot with ozalid integrators; booklets of light sensitive ozalid paper in plasic petri dishes (Friend 1961). One integrator was placed on a leveled area in the center of each plot for 24 hours on 6 September 1987.

Analysis of variance was used to test treatment differences in biomass production, nitrogen concentration and nitrogen total accumulation, and quantity of light. Comparisons of treatment means were tested using Waller-Duncan K-ratio. A probability value of $P < 0.05$ was used throughout the analyses to test significance of F values. Probability levels were calculated in the SAS Institute Inc. (1987) program. Only significant differences are reported in the text. A simple linear regression was used to examine the relationship of biomass production and quantity of light. Due to inadequate and uneven sample size, statistical analysis of soil moisture data were not performed.

Results and Discussion

This research supports the hypothesis that water and nitrogen are limiting environmental variables that control understory production in *P. ponderosa* forests of northeastern Oregon. The greatest response occurred when water + nitrogen were added to the forest floor (Figure 3). Water + nitrogen produced (1031.2 kg ha^{-1}) 16 and 18 percent greater biomass than nitrogen (888.6 kg ha^{-1}) and water (870.6 kg ha^{-1}) treatments and 36 percent more than the control (756.7 kg ha^{-1}). However, the addition of water and nitrogen in separate treatments produced only 15 and 17 percent more understory biomass, respectively, than the control treatment. In the water + nitrogen treatment, addition of water facilitated the uptake of nitrogen to understory plants. This synergistic effect of nitrogen uptake enhanced by higher soil moisture has been documented in a competition

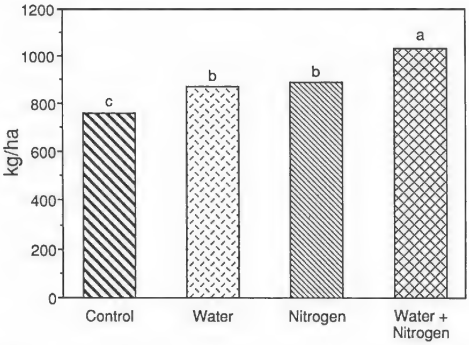

Figure 3. Understory biomass (kg ha^{-1}) response to treatments. Means with the same letter are not significantly different. Standard error of treatment means is ±14.74 kg ha^{-1}.

study using trenches conducted in the same experimental blocks of this study (Riegel 1989).

Irrigating plots increased soil moisture by 41 percent (seven percent difference between watered and non-watered treatments) in the upper third of the profile (0-20 cm depth) where the greatest root competition occurs (Snider and Miller 1985, Svejcar 1986) (Table 1). Addition of soil water increased soil water content to similar levels measured in trenched plots (Riegel 1989) in the 0-20 cm depth. In the mid (20-40 cm) and lower third (40-60 cm) soil depths, adding water also increased soil moisture, but generally less than in the upper third of the profile.

TABLE 1. Volumetric soil moisture (%) (means and standard deviations) measured 24 hours after irrigation within water and non-water treatments.

	Soil Depths (cm)		
Treatments	0-20	20-40	40-60
May 21, 1987 (n = 22)			
Watered (water and water + nitrogen)	23 (5)	20 (3)	19 (3)
Non-Watered (nitrogen and control)	15 (2)	18 (6)	18 (4)
Differences between treatments	8	2	1
June 4, 1987 (n = 5)			
Watered (water and water + nitrogen)	29 (8)	30 (18)	20 (3)
Non-Watered (nitrogen and control)	22 (3)	19 (8)	20 (1)
Differences between treatments	7	11	0

Carex nitrogen concentrations significantly increased in both nitrogen and water + nitrogen treatments with 35 percent more tissue nitrogen concentration than the control (Table 2). Tissue nitrogen concentration did not respond to increased soil water as compared to the control. Nitrogen total accumulation of biomass among treatments was not statistically different, although treatments were higher than the control. *Carex* uptake of nitrogen in the trench treatment (Riegel 1989) produced a similar response. Nitrogen concentrations of *Carex*

TABLE 2. Total nitrogen tissue concentration (%) of *Carex geyeri* foliage and content (kg ha^{-1}) of biomass (means, standard deviations, and standard errors) by treatments. Means with the same letter are not significantly different ($P < 0.05$).

	Nitrogen	Water	Water + Nitrogen	Control
Nitrogen Concentration of *Carex geyeri*	1.33 a	1.04 b	1.32 a	0.98 b
SD	0.15	0.23	0.12	0.24
SE	0.04			
Nitrogen Content of Biomass	11.82 a	9.05 a	13.61 a	7.42 a
SD	5.14	3.30	1.74	2.75
SE	1.50			

in the non-thinned/trenched plots were 1.31 percent in 1987, only 2 percent less than plant tissue nitrogen in the nitrogen fertilized treatments. These responses of increased nitrogen concentration, total accumulation and biomass production are due to a synergistic effect, i.e., uptake of nutrients from the soil were enhanced by the additional soil water in the water + nitrogen and trenched treatments (Jarrell and Beverly 1981, Riegel 1989). However, tissue N concentrations were nearly equal in both nitrogen treatments, but the addition of water in the water + nitrogen treatment promoted more growth. Increased biomass production in the nitrogen treatments may have been aided by increased nitrogen availability early in the growing season, when water was not limiting. Plants growing in fertilized plots appeared darker green and also regrew faster after defoliation than the water or control treatments.

Information on the effect of irrigating and fertilizing herbaceous wild land plants is limited. In an agroecosystem, Singh *et al.* (1979) reported unirrigated *Triticum aestivum* (wheat) did not respond to a nitrogen application greater than 80 kg N ha^{-1}, whereas on irrigated plots response to nitrogen was linear up to 120 kg N ha^{-1}. In our experiment, where water and nitrogen treatments had nearly equal biomass production, the addition of water decreased soil moisture limitation but apparently increased the nitrogen requirement. When plant growth and yield are limited by available moisture the nitrogen requirement is relatively low. If water is applied and growth is increased, the

nitrogen requirement may also increase. Protein synthesis is typically reduced by water stress (Hsiao 1973, Hsiao and Acevedo 1974) and the activities of some enzymes involved in nitrogen metabolism are decreased although others are increased (Todd 1972).

Pumphrey's (1980) findings reinforce our results, that the effect of a nitrogen addition to this system is enhanced when soil moisture is not limiting for plant uptake. When soil moisture is low, nutrient movement to the root surface and uptake are reduced (Marschner 1986). In a study conducted adjacent to our research area, Pumphrey found that spring precipitation correlated most closely with yield of both nitrogen fertilized (67 kg N ha^{-1}) and non-fertilized plots of introduced grasses. April precipitation correlated with yield higher than any other month, for both fertilized ($r = 0.74$) and non-fertilized ($r = 0.42$) treatments. Utilization of water and nutrients during the early growing season takes optimum advantage of this weather pattern. Reducing nitrogen deficiency by fertilizing allowed the grass to be more responsive to precipitation and subsequent higher soil moisture levels.

Other research has demonstrated that sulfur and phosphorus may also limit understory biomass production in this region (Freyman and van Ryswyk 1969; Geist 1971, 1974, 1976a, 1976b, 1977; Geist and Strickler 1978; Klock *et al.* 1975). *Calamagrostis rubescens* fertilized with ammonium and nitrate applied at 100 and 200 kg N ha^{-1} increased biomass production by factors of 1.25 and 2.25 during the year of application (Freyman and van Ryswyk 1969). This response was increased when S (gypsum) was applied with nitrogen. A *Dactylis glomerata* (orchard grass) stand fertilized with ammonium sulfate at a rate of 92 kg N ha^{-1} produced four times more biomass than ammonium nitrate treated plots at the same rate and seven times the unfertilized yield of 213 kg ha^{-1} in the first year (Geist 1976a). Though we did not measure S and P concentration in the soil, *Carex* tissue concentrations of these nutrients were reported higher in plots where tree root competition had been reduced (Riegel 1989).

Light (PAR) does not appear to be limiting understory production in these forests as there was no relationship to light quantity and biomass production. Correlation between biomass and light (PAR), measured on each plot, were not significant ($r^2 = 0.01$). Differences in light levels between treatments were also not significant (Table 3). Plots were distributed in a random stratified procedure which accounted for a 13 percent range in quantity of light that understory vegetation receives. Though we did not increase light as we did with water and nitrogen, results from our thinning study where light was increased demonstrated that the understory biomass did not respond to higher light intensities caused by opening the stand from commercial thinning (Riegel 1989).

TABLE 3. Light, photosynthetic active radiation-PAR (μmol m^{-2} day x 10^6) (means, standard deviations, and standard errors), measured at ground level. There were no significant differences between treatments.

Nitrogen	Water	Water + Nitrogen	Control
12.82 x 10^6	12.22 x 10^6	11.65 x 10^6	12.81 x 10^6
SD 39.34 x 10^6	38.24 x 10^6	7.40 x 10^6	64.30 x 10^6
SE 2.69 x 10^6			

It is doubtful that adding water and nitrogen fertilizer had the same effect as trenching, thus limiting the comparisons of these studies. Severing tree roots decreased soil water depletion rates in the trenched plots throughout the growing season, as compared to non-trenched plots. Besides increasing nitrate and mineralizable nitrogen from the addition of severed tree roots following trenching, many other belowground processes were altered (Riegel 1989). Also, within trenched plots there were no tree roots competing for water and nitrogen. In this experiment, however, tree roots were competing for nitrogen and water which may explain why the response was not as great as in the trenched plots.

Understory vegetation, composed primarily of native herbaceous species, is primarily limited both by water and nitrogen. Without adequate soil moisture, nutrient uptake and plant water relations may limit growth, particularly in years of below average precipitation. Prudent forest and range managers should consider the role overstory competition plays in limiting resources that control understory vegetation growth to insure sustained multiple-resource productivity. Continual resource extraction in nitrogen limited systems may lead to decreased long term productivity.

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Pattern and Color Aberrations in Pelages of *Scapanus townsendii*

Abstract

This study was undertaken to determine the prevalence of aberrantly marked pelages in *Scapanus townsendii* and to ascertain if the aberrant coloration was an additive as suggested by others. Among 663 museum specimens of *Scapanus townsendii* examined, 197 had aberrantly marked pelages and were classified according to the extent and color of the aberrantly pigmented splotches. We found 154 specimens with 1 to several small white spots; 33 with 1 to 3 large yellowish splotches that occupy from <1 to 100 percent of the pelage; 3 with yellowish splotches on predominantly grayish pelages; 5 with pelages mottled grayish, brownish, or yellowish in various combinations; 1 nearly white; and 1 with a uniquely variegated pattern. These colormorphs likely were not the result of additives, but possibly were of genetic origin; did not differ in prevalence among states within the geographic range of the species; and, in some instances, likely were selected against.

Introduction

Although records of occurrence of atypical colormorphs are common for talpids in Europe and eastern North America (Wilson 1860, Barrett-Hamilton 1910, Scheffer 1910, Jackson 1915, Cockrum and Meinkoth 1942, Cooper 1953, Husson and van Heurn 1959, Godfrey and Crowcroft 1960, Skoczeń 1961) reports of such variation in *Scapanus* are rare. A *S. latimanus* with a light cinnamon-yellow pelage (Miller 1921), 2 albino *S. orarius* (Svihla 1939, 1941), and albino (Klein 1944), piebald (Bachman 1839), and iridescent (likely a misidentified *S. latimanus;* Merriam 1885) *S. townsendii* have been described.

On the basis of a collection from a single locality of 25 *Scalopus aquaticus* that contained 18 atypical colormorphs, Jackson (1915:18) suggested that color variation was a dominant character inherited in a "Mendelian ratio"; however, Miller (1921) believed that coat-color inheritance in moles was more complex. Subsequently, Eadie (1954) suggested that some pelage color aberrations in *Parascalops, Condylura, Scalopus,* and possibly *Scapanus,* were the result of staining by products of sudoriferous glands and were related to age and breeding condition of individual specimens. He further indicated that these glands were larger and most abundant on the snout, chin, and wrist, sites at which atypical pelage coloration commonly was observed; glands were smaller and less abundant on the venter and least abundant on the dorsum and along the sides. In *Condylura,* products of the sudoriferous glands reportedly resemble "ceruminous wax of the human ear—both in texture and color" (Eadie 1954:187), and, under magnification, in intensely colored areas, were visible on hairs of fresh specimens as particles of dried colored material. Eadie (1954) further suggested that glandular stains in regions where normal pigments were reduced genetically might account for aberrant pelage colormorphs described in the literature on talpids. Seemingly, Eadie's (1954) report was interpreted to indicate that all pelage coloration in American moles splotched with orange or yellow was attributable to glandular secretions and was totally without genetic basis (Godfrey and Crowcroft 1960; Yates and Pedersen 1982). Being familiar with the bronze wash on the throat, chin, and wrists of some *S. townsendii,* we failed to comprehend how a translucent yellow or orange waxy material could mask the usual purplish-black coloration of other regions of the pelage.

Herein, we report on the types and relative frequencies of pelage color variations in *S. townsendii,* on seasonal and geographic distribution of aberrantly colored specimens, on other biological properties of a sample of aberrantly colored moles, and on our interpretation of the origin and significance of these color and pattern aberrations of the pelage.

Methods

We examined 663 *Scapanus townsendii* from throughout the geographic range of the species (Hall 1981); 197 had aberrantly colored pelage. Specimens examined are on deposit in the National Museum of Natural History (USNM); Oregon State University, Department of Fisheries and Wildlife mammal collection (OSUFW); Portland State

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University, Department of Biology; University of British Columbia; University of California, Museum of Vertebrate Zoology (MVZ); University of Connecticut at Storrs; University of Kansas, Museum of Natural History (KU); University of Minnesota, J. F. Bell Museum of Natural History; University of Oregon (UO); University of Puget Sound, Museum of Natural History (PSM); University of Washington, Burke Memorial Museum. Curators of mammal collections at Humboldt State University, San Diego Museum of Natural History, and the American Museum of Natural History reported no specimens with abberrantly colored pelage on deposit at their institutions. M. Morrison examined 16 *S. townsendii* skins in the Los Angeles County Museum for us and reported none with aberrant pelage color.

Aberrant color patterns were sketched on outline diagrams of dorsal and ventral surfaces of moles or described in detailed notes. Colors of both the aberrantly colored patches and typically colored areas were obtained by comparison with Munsell Color Charts (Munsell Color 1975). Hue, value, and chroma were recorded directly on the diagrams or in notes, and are reported herein parenthetically in that order. Sex, and date and locality of collection, were recorded from specimen tags.

We removed 3 to 4 hairs from each of 3 specimens (OSUFW 712, OSUFW 6030, and OSUFW 6857) and, after mounting them on slids with Permount, examined them at 100X under a compound microscope. Hairs of selected individuals were examined *in situ* under a dissecting microscope. During preparation of one specimen (OSUFW 7111), the skin was washed in acetone to remove any glandular secretions present on the pelage.

Results

On the basis of pigmentation of individual hairs, and of extent and color of aberrantly colored areas of pelage, each specimen was classified into 1 of the following categories:

Type 1

Type 1 specimens (n = 154) were characterized by 1 to several small white (10YR 8/1; 10YR 8/2), pinkish white (7.5YR 8/2), or very pale-brown (10YR 8/3) spots, usually <5 mm in diameter, but often in close proximity to or touching to form irregular patterns or strings 6 to 12 mm long on black (10YR 2/1) dorsal and black or very dark-brown (10YR 3/1) ventral pelages (Figure 1). Individual hairs within the aberrantly colored spots appeared to lack black masses of pigment (Williams 1938) throughout their length. This type seems to correspond with "aberratio coloris *subpunctulata*" in the classification of colormorphs of *Talpa europaea* by Husson and van Heurn (1959).

Sixty-nine females, 82 males, and 3 of undetermined sex were included in Type 1. Female and male specimens with Type 1 markings were collected in all months of the year; the sex ratio was nearly even (1:1.19 in favor of males). The frequency of occurrence of this type was not consistent among portions of the geographic range of the species (X^2 = 22.69; $d.f.$ = 2; $P < 0.05$) as the pelage of 53 (18.0%) of 295 individuals collected in Washington, 13 (61.9%) of 21 individuals in California, and 82 (24.4%) of 336 individuals in Oregon exhibited the small light-colored spots. One male Type 1 specimen we examined (OSUFW 7576; Cloverdale, Tillamook Co., Oregon) was a nestling. In southwestern Oregon, 29.4 percent (n = 10 of 34) of the specimens were spotted, in the Portland, Oregon-Vancouver, Washington area, 22.7 percent (n = 15 of 66) were spotted, and in the Tacoma-Olympia, Washington area, 7.7 percent (n = 10 of 130) were so marked.

Type 2

Type 2 specimens (n = 33) had 1 to 3 pale yellow (2.5Y 8/4), yellow (10YR 7/6), reddish yellow (7.5YR 8/6, 7.5YR 7/6, 7.5YR 7/8), or very pale-brown (10YR 8/3, 10YR 8/4) splotches on black (10YR 2/1) dorsal and black or very dark-brown (10YR 3/1) ventral pelages. Splotches were irregular in shape, but commonly consisted of a blaze on the forehead, a larger stigma on the pectoral region, and occasionally a spot on the lower abdomen (Figure 1). The yellowish coloration covered from <1 to 100 percent of the pelage. Individual hairs in aberrantly colored regions either lacked masses of black pigments between medullary air cells or the size of the masses were reduced greatly; none had visible granules of pigments in the cortex as described for hair of normal-colored pelages (Miller 1921, Williams 1938). However, the yellowish coloration was somewhat more intense (increased chroma) on the expanded tips than on more proximal portions of hairs in the splotched regions.

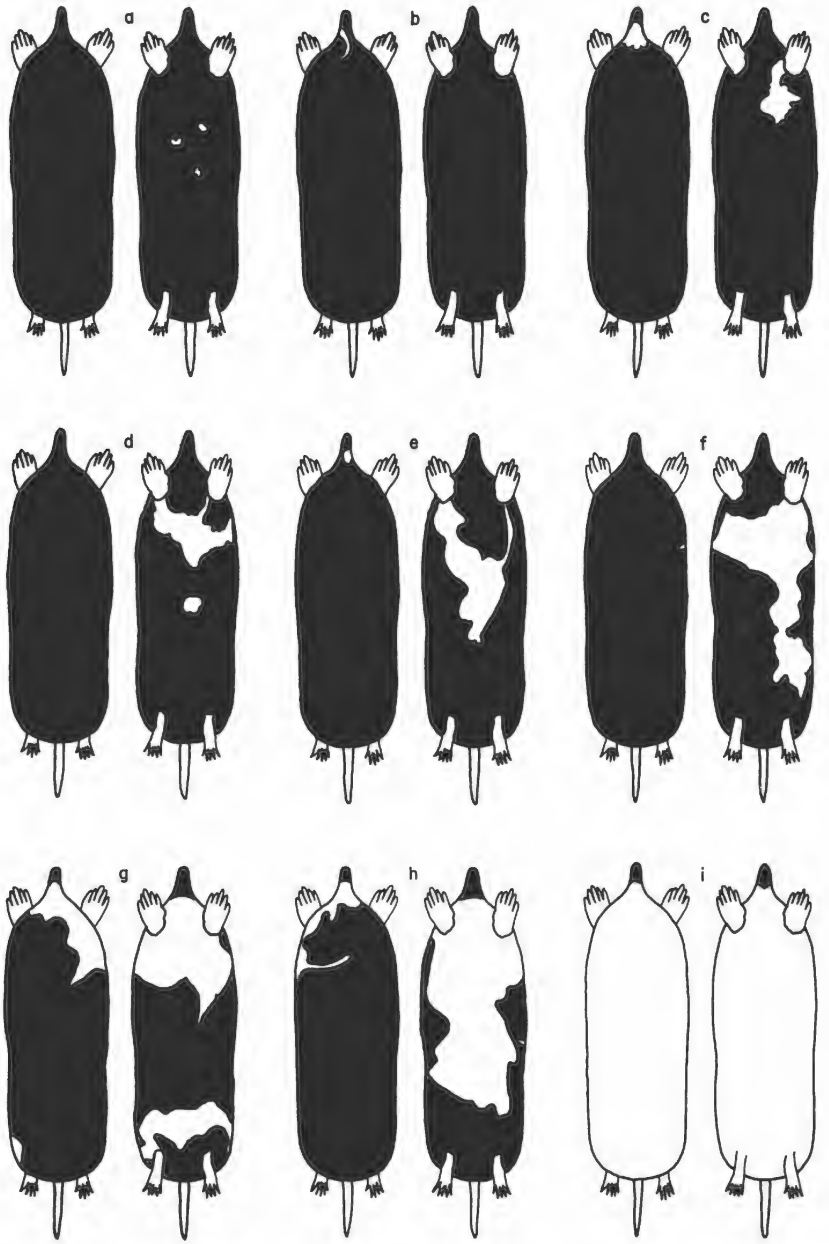

Figure 1. Diagrams depicting aberrant pelage-color patterns (black areas represent normal pelage color) in 9 *Scapanus townsendii:* a, Type 1 colormorph with three white spots on the venter, female, OSUFW 6038. b-i, Type 2 colormorph arranged in order of increasing amounts of yellowish pelage: b, female, OSUFW 6034; c, male, OSUFW 6042; d, male, OSUFW 6035; e, male, OSUFW 6040; f, female, USNM 262275; g, male, OSUFW 6857; h, male, OSUFW 3777; i, male, OSUFW 2618. Note that yellowish markings occur most frequently on the forehead, chest, and abdomen, and are larger and more conspicuous on the venter than dorsum.

Type 2 specimens probably conformed most closely with the "aberratio coloris *innominabilis*" classification of Husson and van Heurn (1959). One specimen (OSUFW 2618), entirely reddish yellow (7.5 YR 7/6) on the dorsum and very pale-brown (10YR 8/4) on the venter, was classified as Type 2 because it seemed to be the extreme in a graded series of moles with various amounts of yellowish pelage (Figure 1b-i). Husson and van Heurn (1959) likely would have classified the specimen as "aberratio coloris *cremea*." Because the splotches, although irregular in shape, occurred most frequently in the pelage of the forehead, chest, and abdomen, Type 2 specimens (except perhaps OSUFW 2618) correspond to the "piebald" condition described by Searle (1968). One Type 2 specimen (PSM 6823), a male collected in the Puyallup Valley, Washington, 28 March 1957, exhibited a molt line that bisected a triangular-shaped splotch left of midline on the venter in the pectoral region. The yellow (10YR 8/6) color on both sides of the molt line was identical.

Ten females, 20 males, and 3 of undetermined sex were included as Type 2. The sample of 30 of known sex was not biased significantly (X^2 = 3.33; $d.f.$ = 1; $P > 0.05$). Type 2 specimens were collected in January, May, June, July, September, October, and November. Geographic distribution of the aberrantly colored specimens tended to be clumped; 9 were collected in the vicinity of Tillamook, Oregon (KU 52686, 52687, 52692, OSUFW 6029, 6031, 6034, 6035, 6040, 6042), 5 in the Corvallis-Eugene, Oregon area (OSUFW 716, 3738, 6857, PSM 11960, UO no number), and only 1 in the southwestern part of the state (OSUFW 3777). In Washington, 9 specimens were from the Tacoma-Olympia area (PSM 881, 1134, 4636, 5991, 6823, 7652, 7653, 8380, USNM 288627). Other Type 2 specimens examined were OSUFW 2618, 7259, 7735, MVZ 19117, 58839, PSM 7288, 7291, 20566, and USNM 262275.

Type 3

The pelage of Type 3 specimens (n = 3) had yellowish-colored patches similar to Type 2 specimens, but on a gray (2.5Y 5/2, 5YR 5/1, 7.5YR 4/0, 10YR 5/1, 10YR 4/1) or brown (7.5YR 6/0) dorsum and gray (10YR 6/1) or light gray (10YR 7/1) venter. Three males (OSUFW 713, 6030, 6039), from the vicinity of Tillamook, Tillamook Co., Oregon, were included in this category. Individual hairs in aberrantly colored regions appeared to be somewhat more intensely colored (increased chroma) on the expanded tip. Hairs in grayish and brownish regions had reduced masses of black pigment, whereas masses were absent in the yellowish regions. Type 3 specimens of *S. townsendii* likely would be considered "aberratio coloris *innominabilis*" in the classification scheme devised by Husson and van Heurn (1959).

Type 4

Type 4 specimens (n = 5) had mottled pelage including gray (10YR 5/1, 7.5YR 5/0, 10YR 7/2, 10YR 6/2, 10YR 3/1, 10YR 6/1), brown (7.5YR 5/4, 10YR 4/3, 10YR 7/3, 10YR 8/3), grayish brown (10YR 6/2, 10YR 3/2), and yellow (10YR 7/6) in various combinations. The dorsum and venter were similar. Overall brownish-gray coloration was formed either by individual hairs with gray (10YR 3/1) or very dark-gray (7.5YR 5/0) bases and light brownish-gray (10YR 6/2) or light olive-brown (2.5Y 5/4) tips (1 male, OSUFW 6044, from Blaine, Tillamook Co., and 1 of undetermined sex, OSUFW 714, from Tigard, Washington Co., Oregon) or by individual hairs with white (10YR 8/1) bases and dark grayish-brown (10YR 4/2, 10YR 3/2) tips (1 male, OSUFW 7389, from 4.5 mi. S, 6.5 mi. W Albany, Linn Co., and 1 female, OSUFW 7898, from 3 mi. W. Monroe, Benton Co., Oregon). These specimens conformed most closely with those categorized as "aberratio coloris *cordida* and *nebulosa*" by Husson and van Heurn (1959). One female Type 4 specimen we examined (PMS 9735; from 2 mi. W. Tillamook, Tillamook Co., Oregon) possessed dark-tipped hairs of 2 lengths over the entire body producing an effect similar to that of agouti banding.

Type 5

Pelage of the single Type 5 (OSUFW 715, undetermined sex, from Noti, Lane Co., Oregon) specimen was white (2.5YR 8/2) on the dorsum and rump shading to yellow (10YR 7/6) on the head and white (10YR 8/2) on the venter shading to reddish yellow (7.5YR 7/6) in the pectoral and throat regions. We suspect that an albino *S. townsendii* referred to by Klein (1944) belonged in this category, but we were unable to locate this specimen for examination. Neither Husson and van Heurn (1959) nor Skoczeń (1961) reported examining predominantly white *T. europaea*.

Type 6

A male (OSUFW 7111) Type 6 specimen, from Tillamook, Tillamook Co., Oregon, exhibited the most garish pattern among the aberrantly colored *S. townsendii* examined. The head (except for a grayish-brown sigma-shaped blaze), the left shoulder, and most of the venter were reddish yellow (7.5YR 7/8) blending to very pale-brown (10YR 8/4) and yellow (10YR 8/6). The remainder of the dorsum posterior of a diagonal line from the right shoulder to the left lower thoracic region, flanks, and anal region were grayish brown (2.5YR 5/2). Individual hairs in the latter region had light gray (7.5YR 7/0) bases; about 90 percent of the hairs had yellow (10YR 8/6) tips and about 10 percent had dark brown (10YR 2/2) or black (10YR 2/1) tips. About half of the hairs with brown or black tips had a similar dark brown band midway along the shaft. The latter band was not sharply defined and seemed nearly to disappear with changes in the angle of illumination, so possibly was of structural rather than of pigmentary origin (Searle 1968). These characteristics remained the same before and after the skin of the specimen was washed in acetone.

Discussion

Because of the relatively restricted breeding season in *S. townsendii* (February to April, Moore 1939; January to April, Pedersen 1963), we believe absence of a strong seasonality in the occurrence of either Type 1 or Type 2 colormorphs in collections is evidence that the aberrancies are not related to the reproductive cycle. This, combined with evidence derived from the Type 2 specimen (PSM 6823) with identical coloration on both sides of a molt line that divided a yellowish splotch, and from those specimens possessing hairs with white or light gray bases interspersed with yellowish hairs and the Type 6 specimen (FW 7111) whose aberrant pelage-color characteristics did not change after being washed in a solvent, indicates that the color was not derived from waxy secretions from sudoriferous glands.

Searle (1968:215) suggested that described colormorphs in *T. europaea* provided "... evidence of mutation with respect to nearly all the major allelomorphic series and also the possibility of a sex-linked yellow...." Because several similar colormorphs occurred among specimens in our sample, we believe that coat-color variants described for *S. townsendii* similarly represent mutations at various loci.

The significant differences in proportions of samples of *S. townsendii* collected in Washington, Oregon, and California with Type 1 aberrancy and the clumped distribution observed among Type 1 specimens in Oregon and Washington suggest that the frequency of the genotype differs among populations. Because white spotting in *S. townsendii* was overlooked easily even in good light, we doubt that "selection for the unusual" or "selection for the typical" by collectors would explain differences noted. However, the other colormorphs deviated markedly from the normal pelage coloration in *S. townsendii;* likely they would be preserved with much greater frequency by collectors than they occurred in populations. The relatively large number of aberrantly colored specimens collected near Tillamook, Eugene, Corvallis, and Portland, Oregon, and near Tacoma and Olympia, Washington, where collectors have been active for many years, may be explained by "selection for the unusual."

In *T. europaea,* the prevalence of aberrant colormorphs reportedly was about 1:1,000 in Poland (Skoczeń 1961), 1:1,600 in Italy (Stein 1950), and 1:300 in The Netherlands (Husson and van Heurn 1959). Similar information for *S. townsendii* is not available because, unlike *T. europaea,* it is not harvested for its fur. Only 1 of >1,200 (L. W. Kuhn pers. comm.) *S. townsendii* collected by Giger (1965*a*) and Pedersen (1963) in the vicinity of Tillamook, Oregon, was marked conspicuously (1 Type 3 specimen); however, 5 Type 1, 5 Type 2, 3 Type 3, 1 Type 4, and 1 Type 6 museum specimens we examined were from that locality. This supports our contention that specimens on deposit in museums are not representative samples of populations in regard to the prevalance of aberrant colormorphs.

Although Searle (1968:247) reported that "... white-spotting mutations abound in mammals, but most have adverse pleiotropic effects," the high prevalence (23.3%) of Type 1 colormorphs in our sample suggests that such effects in *S. townsendii,* if extant, are minor. Thus, the inconspicuousness of the white spotting in Type 1 specimens and the high prevalence of the colormorph in our sample suggest that the mutation does not confer a selective disadvantage; we cannot hypothesize a possible advantage. However, we suggest that the relatively low prevalance of Types 2, 3, 4, 5, and

6 colormorphs in our sample, the relative infrequency of yellowish splotches on the dorsum of Type 2 specimens, and the occurrence of remains of *S. townsendii* in regurgitated pellets of barn owls (*Tyto alba;* Giger 1965*b*) indicate that conspicuous markings in *S. townsendii* likely are selected against.

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The Holocene History of the Red Fox (*Vulpes vulpes*) in Eastern Washington

Abstract

A modern zoogeography of the red fox (*Vulpes vulpes*) in eastern Washington based on historic data, and a conjectured Quaternary zoogeography of the red fox based on its modern distribution there are evaluated with prehistoric data. Red foxes are indigenous to the Pacific Northwest, and have existed there throughout the last 10,000 years, dispersing northward into deglaciated areas early in the Holocene. Eastern Washington's extant foxes may be hybred descendants of indigenous and introduced foxes.

Introduction

In a review of the early 20th century historic zoogeography of red foxes (*Vulpes vulpes*) in the state of Washington, Aubry (1984) concluded: 1) "foxes are infrequently found in [the Columbia Basin during the 20th century, and most of those found are] presumably derived from foxes that escaped from fur farms in the 1930s and 1940s [whereas others found there] probably represent wandering or dispersing individuals" (Aubry 1984:77); 2) the presently extant population of red foxes in northeastern Washington "is descended from introduced animals" (Aubry 1984:77); and 3) a single museum specimen collected in 1923 "constitutes the only evidence that indigenous red foxes occur in southeastern Washington [and probably represents] wandering foxes that were not from an established local population" (Aubry 1984:78).

In his overview of Washington mammals, Dalquest (1948:58, 79) speculated that red foxes in the Cascade Range of Washington took refuge in the southern Cascades during the Wisconsinan glacial episode, and that foxes in eastern Washington took refuge in the Blue Mountains of southeastern Washington during the Wisconsinan. Both populations dispersed northward, Dalquest conjectured, after glacial retreat (during the Holocene).

The bridge linking Dalquest's speculations and Aubry's conclusions is found in prehistoric remains of red foxes. In this paper I review the Holocene (last 10,000 years) record for red foxes in eastern Washington. That prehistoric record as it is now known indicates that Aubry's (1984) conclusions and Dalquest's (1948) speculations are not incompatible, and largely account for the Holocene record.

Methods and Materials

All red fox specimens reported were recovered from archaeological sites. Due to the nature of archaeological research in eastern Washington, the specimens may or may not be representative of the abundance or complete distribution of red foxes there during the Holocene (Grayson 1981, 1984; Lyman 1987b).

My own archaeological data (7 sites) and a review of the published and unpublished mammalian faunal data from eastern Washington and vicinity (182 sites) reveal the presence of red fox remains at 16 sites which span the entire Holocene (Table 1, Figure 1). I do not include the remains reported simply as "fox" by Osborne (1957:119), nor the two reported instances of grey fox (*Urocyon cinereoargenteus*) reported by Deaver (1973;

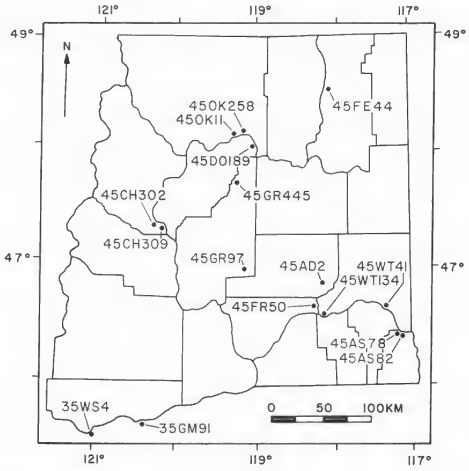

Figure 1. Holocene archaeological sites with remains of red fox (*Vulpes vulpes*) in eastern Washington. County lines shown for reference.

TABLE 1. Summary of Holocene archaeological red fox data in eastern Washington. See Figure 1 for site locations.

SITE	YEARS B.P.	SPECIMENS (N)	REFERENCE
35WS4	10,000-4,000	? (5 individuals)	Cressman *et al.* 1960
35GM91	5,000-150	radius, ulna (2)	Schalk 1987
45GR97	8,700	innominate (1)	Irwin and Moody 1978
45AD2	3,500-150	3 or 4 phalanges, ? (14)	Deaver 1973, Deaver and Greene 1978
45CH309	?	mandible (1)	Lyman, unpub.
45CH302	2,500-500	skull, 3 mandibles, 1 isolated molar, 2 vertebrae, 2 humerii, 2 radii, 4 ulnae, carpal, 4 metacarpals, femur, 2 innominates, tibia (24)	Lyman, unpub.
45OK11	4,000-2,000	phalange (1)	Livingston 1985a
45OK258	4,000-2,000	2 mandibles, 3 isolated molars (5)	Livingston 1985b
45DO189	3,000	humerus (1)	Lyman 1988b
45FE44	9,000-4,400	? (1)	Chance and Chance 1982
45FR50	10,000-8,000	skull (1)	Gustafson 1972
45WT134	4,000-3,500	skull (1)	Lyman, unpub.
45WT41	8,000-6,700	? (1)	Gustafson 1972
45AS78	3,000-100	mandible (1)	Lyman 1976
45AS82	5,000-2,500	mandible, ? (4)	Lyman 1976
45GR445	2,500-2,100	radius, ulna, calcaneum (3)	Lyman, unpub.

Deaver and Greene 1978) and Mead *et al.* (1985). My identifications of bones and teeth as representing *V. vulpes* have been based on the size and morphology of the remains; red foxes tend to be larger, for instance, than other members of the genus. Ingles (1965:339) reports the length of red foxes as 90-100 cm and red fox skulls as 13.7-15.1 cm long. Those same measurements for the kit fox (*V. macrotis*) are 60-84 cm and 10.5-12.2 cm (Ingles 1965:339). The average swift fox (*V. velox*) weighs 2.5-3.5 kg, the average kit fox weighs 2-3 kg, and the average red fox weighs 3-7 kg (Samuel and Nelson 1982).

Because the taphonomic history of a bone assemblage recovered from an archaeological site is difficult to ascertain (Lyman 1987b), the extent to which such assemblages resemble the original fauna from which they were derived cannot be determined (Grayson 1981). It is reasonable to assume, however, that taxa represented in archaeological faunal assemblages lived in the general area of the site of recovery. Typically only bones and teeth of great socio-economic value were transported over great distances by prehistoric peoples (Lyman 1985 and references therein).

Frequencies of red fox remains reported in Table 1 are numbers of identified bones and teeth, with the exception of the record for 35WS4 which was reported as the minimum number of individual animals represented by an unspecified number of bones and teeth. The written record for red fox remains from eastern Washington archaeological sites does not always include which parts of the skeleton were identified, but I have included such information when available in Table 1. The reported bones and teeth represent most major anatomical regions of the body, indicating that while some of the remains may have been transported significant distances, such as phalanges still attached to a hide used for clothing, that is not regularly the case.

None of the 35 (57.4% of total sample of 61) specimens I have identified displays evidence of human modification, such as butchering marks. Similarly, the two specimens reported by Gustafson (1972), the 14 reported by Deaver and Greene (1978), and the six reported by Livingston (1985a, b) apparently do not display butchery marks (with my 35, 93.4% of total sample of 61). Although such negative evidence does not mean people were not responsible for the deposition of any or all of those remains (Lyman 1987a), there is no evidence to prompt me to argue that any of those remains were deposited by people. The fact that the remains were found in archaeological contexts provides

little clarification of this issue (Lyman 1987b). In the following then, I presume the red fox remains discussed were not transported significant distances (>25 km) by prehistoric human hunters, fully realizing this presumption may be false.

Results

There are no known Wisconsinan-aged red fox remains from eastern Washington, but that may be due to the fact that only three faunal assemblages of that age are known from this area (Lyman 1986a). That red foxes were in eastern Washington during the early Holocene (10,000 to 7,000 B.P.) is indicated by remains from four sites. Fox remains from 45FR50 may date as early as 10,000 years ago, remains from 45WT41 as early as 8,000 years ago, and remains from 45FE44 as early as 9,000 years ago. The fact that 45FR50 and 45WT41 are in southeastern Washington and 45FE44 is in northeastern Washington provides support for Dalquest's (1948) conjecture that red foxes occupied mountainous regions in eastern Washington during the last glacial period, then dispersed northward during the Holocene. An early Holocene dispersal might account for the 8,700-year-old remains from 45GR97.

The 10,000-year-old fox remains from 35WS4 suggest that foxes may have taken refuge in the southern Cascades of Washington during the Wisconsinan, just as Dalquest conjectured. These data also suggest a possible early or middle (7,000 to 3,500 B.P.) Holocene dispersal by foxes into the northern Cascade Mountains of Washington, which might also account for the middle Holocene remains from 45OK11 and 45OK258. In addition, the middle Holocene record from 45WT134, plus the possible middle Holocene records from 35GM91, 45OK11, 45OK258, and 45AS82 suggest that red foxes were present in eastern Washington during this relatively warm and dry climatic period (Barnosky *et al.* 1987), even though red foxes tend to avoid hot, dry habitats (see Samuel and Nelson 1982 for a general account).

During the late Holocene (last 3,500 years), red fox remains were deposited at 45AD2, 45CH302, 45DO189, 45AS78, and 45GR445, and possibly at 45GM91, 45OK11, 45OK258, and 45AS82. It is unclear if this apparent increase in frequency of site records over the middle Holocene is due to greater abundances of foxes at this time, or the fact that more late Holocene archaeological remains have been recovered and studied (Lyman 1986a, 1987b).

It is difficult to ascertain whether the Holocene red fox remains described here represent "established local populations" or "wandering" (Aubry 1984) individuals. All remains I have examined represent skeletally mature individuals rather than newborns or juveniles. Recovery of the remains of newborns might be taken as evidence of locally reproducing established populations. Given the low probability for preservation of the remains of newborns of any mammalian taxon in the archaeological record (Lyman 1984), the absence of newborn red fox remains in eastern Washington archaeological sites does not necessarily mean that resident local populations did not exist there.

Aubry (1984) concludes on the basis of historic data that most twentieth century red foxes in eastern Washington are derived from introduced fur farm escapees. The 16 Holocene records reported in Table 1 suggest that modern populations in eastern Washington may also include individuals descended from red foxes that occurred in this region during the Holocene. Whether those indigenous foxes were resident to eastern Washington or resident to contiguous areas, such as the Idaho panhandle and occasionally wandered through eastern Washington, cannot be determined from the available data.

Discussion

The Holocene zoogeography of mammals in Washington has been dynamic (Livingston 1987, Lyman 1986a, 1986b, 1988a, Lyman and Livingston 1983, McCorquodale 1985, Van Vuren 1987). Significant additions to our understanding of that history can be found by careful evaluation of historic records, as Aubry (1984) has shown. But the prehistoric record is also an important source of information, as Fichter and Williams (1967) have shown for red foxes in Idaho. The prehistoric record provides a unique source of information that temporally extends historic data, occasionally prompting conclusions different from those suggested solely by historic data (e.g., Lyman 1988a).

The faunal record as reflected by archaeological data suggests that red foxes were widespread in eastern Washington throughout the Holocene. Those data also are readily subsumed within Dalquest's (1948) conjectured late Quaternary

zoogeography of red foxes. Perhaps the apparently low historic population of indigenous red foxes implied by Aubry's (1984) analysis resulted from the impacts of Euroamerican settlement, particularly given early historical perceptions of them as harmful predators (see Buechner 1953 for other examples). Importantly, it seems clear that modern red fox populations in eastern Washington might not simply be the result of historic introductions.

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Small Mammals in a Subalpine Old-growth Forest and Clearcuts

Abstract

This study examined the differences between small mammal populations in a subalpine old-growth forest and adjacent burned and unburned clearcuts. Small mammals were lived trapped, marked and recaptured weekly during July and August of 1987. Deer mice (*Peromyscus maniculatus*) and chipmunks (*Tamias amoenus*) were most abundant in the two clearcuts; shrews (*Sorex cinereus*) were common in all three habitats; and red-backed voles (*Clethrionomys gapperi*) were common in all but the burned clearcut and the forest edge adjacent to the unburned clearcut. This latter finding may reflect an "edge effect." There were more adult female deer mice and a smaller ratio of juvenile to adult female deer mice in the forest than in the clearcuts. This study suggests that the general effects of clearcutting on small mammals are similar in lowland and subalpine forests, and that edge effects are an important consideration for future research, particularly in old-growth forests.

Introduction

The old-growth coniferous forests of the Pacific Northwest are ecologically unique (Waring and Franklin 1979, Franklin *et al.* 1981), but increasingly fragmented by forest harvesting (Harris 1984). As accessible lowland old-growth stands are depleted, there is increasing pressure to harvest higher elevation forests. Numerous studies have examined the effects of logging on small mammals in lowland, northwestern coniferous forests (Tevis 1956; Gashwiler 1970; Hooven 1971, 1973; Sullivan 1979), but there are few data on impacts in old-growth and subalpine forests. It is important to gain both a better understanding of the ecology of old growth and the effects of cutting these forests in the more extreme subalpine environment. This study was designed to compare small mammal populations and communities of a coastal, subalpine old-growth forest and adjacent burned and unburned clearcut habitats.

Study Area and Methods

The study was conducted in Cypress Provincial Park, just north of Vancouver, British Columbia, in the forested sub-zone of the Sub-alpine Mountain Hemlock Zone (Brooke *et al.* 1970, Lertzman 1989). The area is characterized by a cool, maritime climate with high annual rainfall and winter snowpack, and relatively warm, dry summers.

Trap lines were established on a south-facing slope from 990-1090 m elevation, passing through three habitats: old-growth forest, clearcut, and burned clearcut. The old-growth forest (>1200 years old) was composed of 45 percent *Abies amabilis*, 25 percent *Tsuga heterophylla*, 21 percent *Tsuga mertensiana*, and 9 percent *Chamaecyparis nootkatensis*, with *Vaccinium* spp. dominating the patchy understory shrub layer,and *Rubus pedatus* the most prominent herb (Lertzman 1989).

Immediately down slope of this forest stand was an area clearcut in 1970/71 (K. Lertzman, personal communication). The upper part of the clearcut had 100 percent ground cover, dominated by *Vaccinium ovalifolium*, *V. membrenacium*, and regenerating *A. amabilis*. The lower clearcut had burned shortly after logging (1973), and had less prominent ground cover, dominated by *Salix* spp., *Sambucus* spp., scattered young conifers, *Epilobium angustifolium*, and *Anaphalis margaritacea*, with much soil exposed.

Four parallel trap lines, 15 m apart with 22 Longworth live traps spaced at 15 m intervals on each line, formed a large rectangular grid which covered the three habitats. There were 56 traps in the forest (covering 1.26 ha) and 16 traps (0.36 ha) in each of the clearcuts. Traps were baited with oats and provided with cotton batting for bedding. Animals were ear-tagged at first capture. For each capture, I recorded trap location, tag number, weight, sex, and reproductive condition. I considered animals <13 g at first capture as juveniles and >16 g as adults (no animals were 14 or 15 g). The distinction between lighter and heavier animals corresponded to differences in pelage colour for each species and was presumed to reflect the difference between immature and sexually active animals.

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I trapped two consecutive nights each and every week for 7 weeks between July 8 and August 21, 1987, for a total of 208 trap-nights in each clearcut and 728 trap-nights in the forest. Traps were checked each morning and afternoon while set, and locked open between trapping sessions. Each trapping session thus comprised 2 consecutive nights of trapping or four consecutive trap checks (2 morning and 2 afternoon).

Small population sizes in some instances rendered the Jolly-Seber method of population estimation inappropriate for this study. I thus applied the less preferable (see Nichols 1986) Minimum Number Alive method (Hilborn *et al.* 1976) to estimate population sizes in the three habitats. Population numbers and captures were standardized directly to per ha densities with all individuals captured in a given habitat included in the estimate, regardless of their original habitat origin. Direct conversion to densities is inaccurate because animals living outside of the grid will venture onto the grid occasionally and be trapped there. However, since the grids had nearly similar interior to edge ratios (15 m^2/m for each clearcut grid and 23 m^2/m for the forest grid), direct conversion was reasonable for providing comparable measures as long as it was kept in mind that clearcut estimates were likely slightly overestimated relative to the forest. I applied Friedman's nonparametric analysis of variance (Zar 1984) to compare between habitats the weekly density estimates that were derived from each of 7 trapping sessions.

Results

I trapped five small mammal species during the study: deer mice (n=53), southern red-backed voles (n=35), masked shrews (*Sorex cinereus;* n =18), yellow-pine chipmunks (*Tamias amoenus;* n=6), and an ermine weasel (*Mustela erminea;* n=1). Douglas squirrels (*Tamiasciurus douglasii*) were frequently observed in the forest, but none were trapped. Only voles and deer mice were captured repeatedly in sufficiently large numbers to examine statistically. Abundance of shrews and chipmunks were estimated from total captures (Table 1) since difficulty was encountered in determining recaptures for these species.

Mean weekly population density estimates are listed in Table 1. Weekly population densities of deer mice were more than twice as great on the unburned and burned clearcuts than in the forest (Friedman's test, $X^2 = 11.238$, $0.001 < p < 0.002$, d.f. = 2). Some deer mice moved between habitats (1 juvenile from unburned to burned clearcut, 2 juveniles and 1 adult from burned to unburned clearcut, and 2 juveniles from forest to burned clearcut), but this movement was unidirectional and therefore did not affect the density estimates. Sex ratios were similar between habitats when adults and juveniles were combined. There were equal numbers of males and females on each of the clearcuts ($X^2 = 0.50$, $p > 0.25$, d.f. = 1 for burned; $X^2 = 0.0$, $p > 0.5$, d.f. = 1 for unburned). However, there were more first-captures of adult females (N=13) than of adult males (N=3) in the forest ($X^2 = 6.25$, $p < 0.025$, d.f. = 1). In fact, only one adult male was trapped for >2 weeks there. Analysis of deer mice first captures revealed that there was a significantly greater proportion of juveniles to adult females in the burned clearcut (0.81 or 13 of 16) compared to the forest (0.43 or 10 of 23) ($X^2 = 5.56$, $P < 0.025$, d.f. = 1). The proportion of juveniles to adult females was not significantly different between the unburned clearcut and forest ($X^2 = 0.12$, $p > 0.5$, d.f. = 1) and the two clearcuts ($X^2 = 2.82$, $p > 0.05$, d.f. = 1).

TABLE 1. Mean standardized population densities (#/ha) from 7 weekly estimates (based on the minimum number alive). The total number of animals first-caught in each habitat is listed in parentheses.

	Forest	Unburned cut	Burned cut
Deer mice	10.2 (24)	22.2 (10)	24.6 (19)
Red-backed voles	9.3 (20)	8.3 (12)	1.6 (3)
Shrews	1.5 (13)	0.8 (2)	1.2 (3)
Chipmunks	1.6 (2)	4.4 (2)	5.6 (3)

Weekly densities of red-backed voles in the forest and on the unburned clearcut were similar, but considerably larger than on the burned clearcut (Friedman's test, $X^2 = 7.806$, $0.02 < p < 0.05$, d.f. = 2) where almost no voles were captured (Table 1). Body weight at first capture was not different among habitats ($t = 0.419$, $p > 0.5$, d.f. = 16). The ratio of males to females was equal in the forest ($X^2 = 0.8$, $p > 0.25$, d.f. = 1) and unburned clearcut ($X^2 = 0.33$, $P > 0.5$, d.f. = 1), and there was no difference in the sex ratios between the two habitats ($X^2 = 0.0086$, $P > 0.5$, d.f. = 1).

Shrews and chipmunks were captured in all three habitats (Table 1). Almost all shrews died

at first capture in the traps. If total captures are assumed to be an independent index of relative abundance, shrews were equally abundant in all habitats ($X^2 = 0.730$, $p > 0.5$, d.f. = 2). Chipmunks were most commonly captured in the clearcuts, but individuals were highly mobile and occasionally moved between the forest and clearcuts.

There was no record of vole movement between the forest and clearcuts (there were no voles first caught in the forest which were later captured on either clearcut, and vice-versa). Furthermore, although vole captures were high in both the forest and the unburned cut, there were almost no captures in the 12 traps located in the 35 m of forest nearest the clearcut (Table 2). This difference is significant if one groups the traps by horizontal lines running parallel to the forest edge and compares the number of captures of different individuals in the traps in the three lines nearest the forest edge compared to the 11 lines in the forest interior ($X^2 = 7.58$, $p < 0.01$, d.f. = 1). There was no difference between the forest edge and interior in the number of individual deer mice caught ($X^2 = 1.12$, $p > 0.25$, d.f. = 1).

TABLE 2. Number of individual red-backed voles and total captures of voles (each number indicates the sum of four live traps) every 15 m along the length of the forest grid extending from the clearcut to 200 m into the forest.

	Distance (m) into forest from edge of clearcut													
	5	20	35	50	65	80	95	110	125	140	155	170	185	200
No. individuals*	2	0	1	4	2	3	6	5	3	6	4	5	8	3
Total No. caught*	2	0	1	18	8	11	21	13	5	20	7	15	20	11

*$p < 0.01$ ($X^2 = 7.58$, d.f. = 1), comparison between 3 forest lines nearest edge (5-35 m) and 11 forest lines farthest from edge (50-200 m).
**statistically invalid to test due to repeated captures of the same individuals.

Discussion

This study suggests that the effects of logging on small mammals are similar in subalpine and lowland old-growth forests. Data from the present study support previous observations that deer mice are more common on recently logged and in early successional habitats than in mature forest, and red-backed voles are absent from clearcuts in which adequate vegetation cover has not yet developed (Tevis 1956, Gashwiler 1970, Hooven 1971, Krefting and Ahlgren 1974, Gunther *et al.* 1983, Naylor and Bendell 1983, Scrivner and Smith 1984).

Deer mice were abundant in all three habitats; however, their populations differed qualitatively between habitats. There were greater numbers of adult female than adult male deer mice but a lower proportion of juveniles to adult females in the forest compared to the clearcuts. Populations of *P. leucopus* and *P. maniculatus* on clearcuts have been suggested to be characterized by animals that are behaviorally subordinate in comparison to mice in forest populations (Sullivan 1979, Martell 1983). Linzey (1989) has provided experimental support for this from behavioral studies of *P. leucopus*. The large number of adult females and few young in the forest in this study is also in agreement with work suggesting that territorial adult female deer mice limit juvenile survival and recruitment (Galindo and Krebs 1987). The burned clearcut may have acted as a behavioral sink for subordinate forest deer mice excluded by aggressive adult females in the forest. The two records of juvenile movement from forest to clearcut support this.

But whereas deer mice are habitat generalists, red-backed voles are more characteristic of interior forest dwelling species that require a moist environment and prefer habitats with many of the features characteristic of old-growth forests, such as high densities of rotting logs and stumps, loose forest litter, and sphagnum (Gunderson 1959, Franklin *et al.* 1981). Voles probably avoided the burned clearcut because of the absence of an adequate vegetation cover and moisture. Soils on the burned cut were very dry during the study, with mid-day summer surface soil temperatures as high as 60° C (K. Lertzman, personal communication). The unburned clearcut had sufficiently dense *Vaccinium* cover to maintain the cool and moist microclimate near the ground preferred by voles in summer, as well as provide an abundant supply of berries for food (West 1982). However, the results of this and

other studies of *Peromyscus* cited above indicate that the presence of voles in both habitats does not necessarily indicate that the unburned clearcut and interior forest habitats are similar in quality. More research is needed to determine if the two habitats, in fact, support qualitatively different populations of voles.

Hot, dry summer and cold winter winds penetrating the exposed forest interior at the edge have considerable affect on forest microclimate and vegetation (Ranney *et al.* 1981). For example, conifer seedling survival at one location at this study site near the forest edge was strikingly poor in relation to the deeper forest interior (K. Lertzmann, personal communication). While not conclusive, trapping results from this study suggest that edge habitat (identified to extend between 35 and 50 m into the forest from the clearcut) may be as unfavorable to voles as the highly exposed habitat of a burned clearcut. Other studies (Walters and Lertzman, in preparation) indicate that vegetation associations specific to the interior of old-growth forest are important for determining vole dispersion.

Edge effect increases with edge contrast and, therefore, is maximized with the clearcutting of old growth (Harris 1984). The severe subalpine climate may enhance this effect as well as retard the rate at which lateral canopy extension and shrub and sapling tree growth fill in the edge (Ranney *et al.* 1981). The role of edge effects has important forest and wildlife management implications and is deserving of greater attention as increasing areas of old growth are exposed to clearcuts and reduced to habitat islands (Harris 1984).

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Revision of Biogeoclimatic Units of Coastal British Columbia

Abstract

Tabular and multivariate analyses using subsets of 1299 samples of alpine, subalpine, montane, and submontane, zonal, climax vegetation resulted in a revision and refinement of the biogeoclimatic units for coastal British Columbia originally proposed by Krajina and modified by subsequent workers. The revision conserved the existing four biogeoclimatic zones (Coastal Douglas-fir, Coastal Western Hemlock, Mountain Hemlock, and Alpine Tundra) but increased the number of subzones from two to ten in the Coastal Western Hemlock zone, from two to four in the Mountain Hemlock zone and reduced the number of subzones from two to one in the Coastal Douglas-fir zone. Diagnostic tables, climatic summaries, and ordination results are presented to show relationships among the zones and subzones. Climatic data suggest that the four zones, each characterized by a unique Koppen's climatic type, represent major segments of the regional temperature gradient, while subzones reflect division of this gradient according to continentality, precipitation, and temperature.

Introduction

Biogeoclimatic ecosystem classification (BEC), recently reviewed by Pojar *et al.* (1987), is used both as a research and forest management tool in British Columbia. This paper focuses on zonal classification of the BEC system, at which ecosystems are organized into biogeoclimatic subzones and zones according to similarities in regional climate.

Many ecological classifications have organized ecosystems according to regional climate. Some classifications are based on the results of climatic analysis (e.g., Rauscher 1984, van Groenewoud 1984, Denton and Barnes 1988) while others have adopted the zonal or climatic climax concept to delineate regional climates (e.g., Krajina 1965, Daubenmire 1968, Damman 1979, Bailey 1988). In the latter approach, vegetation is used as a surrogate for climate. The BEC system uses the zonal concept and the vegetation of zonal climax ecosystems to frame biogeoclimatic subzones—classes of ecosystems each presumed to be influenced by roughly the same climate. Zonal ecosystems are those in which the integrated influence of climate on vegetation, soil, and other ecosystem components is most strongly expressed. Climate influences ecosystems most strongly if its effects are modified as little as possible by disturbance, local topography, and physical and chemical properties of the soil. Zonal climax ecosystems must feature (i) intermediate topographic and edaphic conditions in relation to the existing extremes and (ii) the near-climax or climax stage of vegetation development (*op. cit.*).

The original zonal classification for coastal British Columbia, developed by Krajina (1959, 1965, 1969, 1972) was based mostly on dissertation data from the south coast (McMinn 1957, Mueller-Dombois 1959, Archer 1963, Orloci 1964, Cordes 1972, Brooke *et al.* 1970, Kojima 1971). From 1975 to 1985, further sampling was carried out throughout the coast by the Ecological Program Staff of the British Columbia Forest Service, from low to high elevations and across the range of climates (Figure 1). The new data indicated that the original biogeoclimatic subzones were too general (see Table 1) and that the subsequent modifications were local and inconsistent revisions of the zonal classification (e.g., Packee 1974; Klinka *et al.* 1979, 1984).

In the western United States, ecological zones of habitat type classification (Pfister and Arno 1980; Franklin *et al.* 1988) or vegetation zones of plant community classification (Franklin and Dyrness 1973) occupy a similar place in the classification hierarchy as biogeoclimatic zones do in the BEC system (see Ferguson *et al.* 1989). However, the resultant zones are not the same in coastal British Columbia and Alaska-Washington-Oregon.

The aim of this study is to present the result of a refined zonal classification which combines and

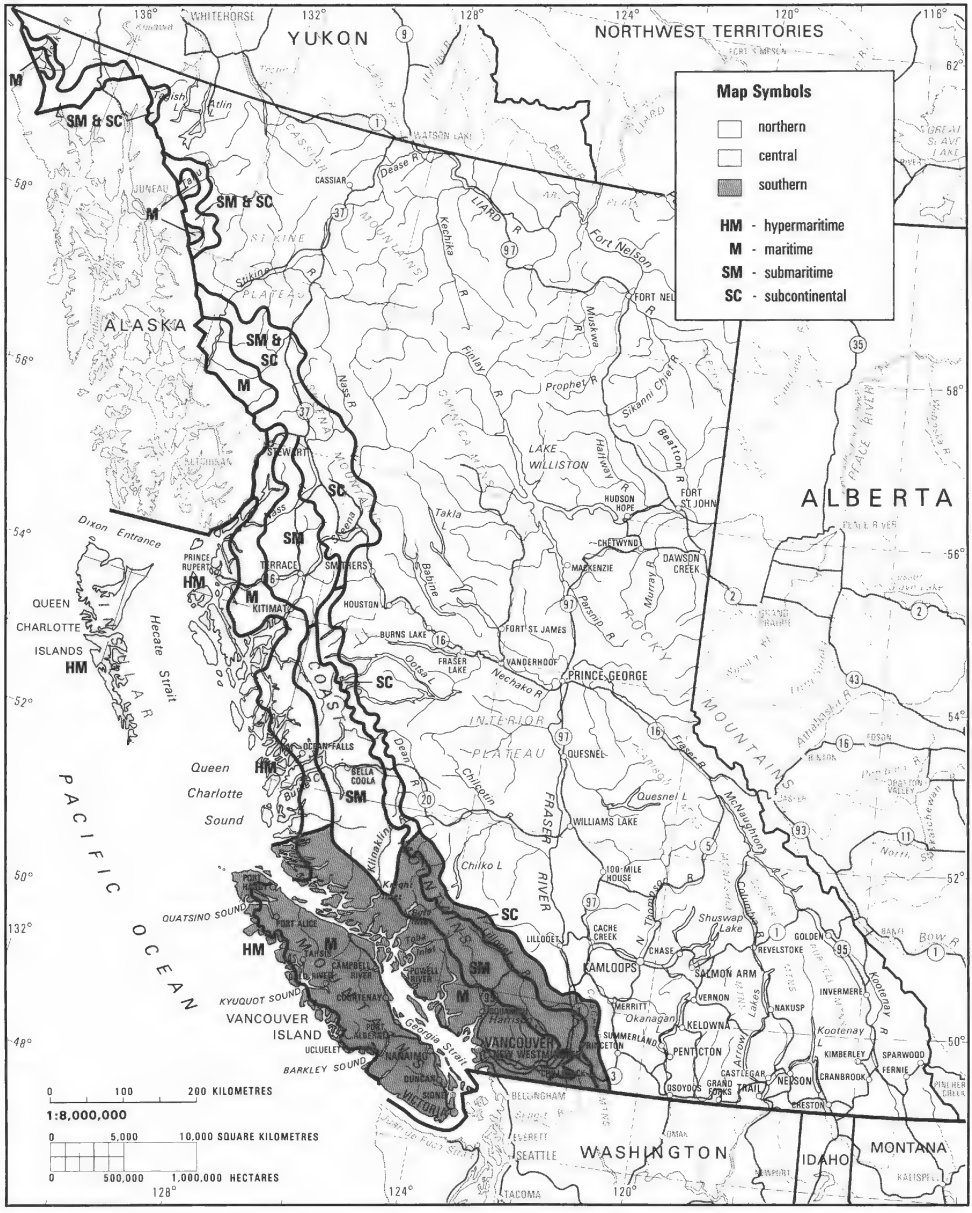

Figure 1. Outline of four continentality strata (hypermaritime, maritime, submaritime, and subcontinental) and three latitudinal strata (north, central, and south) as applied in zonal classification in coastal British Columbia.

TABLE 1. Biogeoclimatic zones and subzones of coastal British Columbia, and correspondence between biogeoclimatic zones and the ecological zones of habitat type classification.

Revised units **Zone** Subzone	Krajina (1969) **Zone** Subzone	Corresponding ecological zones of habitat type classification to biogeoclimatic zones
Coastal Douglas-fir (CDF)	**Coastal Douglas-fir** (CDF)	*Abies grandis* *Pseudotsuga menziesii* *Quercus garryana* *Thuja plicata*[2]
Moist Maritime CDF (CDFmm[1])	Drier CDF (CDFa)	
Coastal Western Hemlock (CWH)	**Coastal Western Hemlock** (CWH)	*Abies amabilis*[2]
Wet Hypermaritime CWH (CWHwh)	Wetter CWH (CWHb)	*Chamaecyparis nootkatensis*[2]
Very Wet Hypermaritime CWH (CWHvh)	Wetter CWH (CWHb)	*Picea sitchensis* *Thuja plicata*
Very Dry Maritime CWH (CWHxm)	Wetter CDF (CDFb), Drier CWH (CWHa)[2]	*Tsuga heterophylla*[2]
Dry Maritime CWH (CWHdm)	Drier CWH (CWHa)[2]	
Moist Maritime CWH (CWHmm)	Wetter CWH (CWHb)	
Wet Maritime CWH (CWHwm)	Wetter CWH (CWHb)	
Very Wet Maritime CWH (CWHvm)	Wetter CWH (CWHb)	
Dry Submaritime CWH (CWHds)	Drier CWH (CWHa)	
Moist Submaritime CWH (CWHms)	Wetter CWH (CWHb)	
Wet Submaritime CWH (CWHws)	Wetter CWH (CWHb)	
Mountain Hemlock (MH)	**Mountain Hemlock** (MH)	*Abies amabilis*[2]
Parkland Hypermaritime MH (MHph)	Parkland MH (MHb)	*Abies lasiocarpa*[2]
Forested Hypermearitime MH (MHfh)	Forest MH (MHa)	*Chamaecyparis nootkatensis*[2] *Tsuga mertensiana*
Parkland Maritime MH (MHpm)	Parkland MH (MHb)	
Forested Maritime MH (MHfh)	Forest MH (MHa)	
Alpine Tundra (AT)	**Alpine Tundra** (AT)	
Maritime AT (ATm)	Coastal AT (ATa)	

[1]The lowercase symbols used for subzones designate precipitation (x—very dry, d—dry, m—moist, w—wet, v—very wet), continentality (h—hypermaritime, m—maritime, s—submaritime), and physiognomy (p—parkland, f—forested).
[2]in part.

analyzes all the coastal zonal vegetation data available to date. The tabular method was used to classify zonal climax ecosystems and multivariate methods were used to analyze floristic relationships. The results include diagnostic vegetation and selected climatic characteristics of biogeoclimatic zones and subzones and an evaluation of floristic relationships.

Materials and Methods

The complete data set included 1299 sample plots selected, from over 5000 plots using the topographic and edaphic criteria given in Pojar *et al.* (1987, p. 127), to represent zonal, late-seral ecosystems (usually mature forests older than 200 years). The data were obtained from dissertations (McMinn 1957; Orloci 1961, 1964; Archer 1963; Brooke *et al.* 1970; Kojima 1971; Cordes 1972; Roemer 1972; Klinka 1976; Beese 1981; Roy 1984; Kabzems 1985), research reports (Lewis 1982, 1985), and from unpublished survey results on file with the B.C. Forest Service.

We have used the same methods of sampling and vegetation description as outlined in Brooke *et al.* (1970). At each 0.04 ha plot, chosen to represent a relatively uniform community, all plant species present in the tree, shrub, herb, and moss strata were identified and their cover was estimated using the Domin-Krajina scale of species significance (Mueller-Dombois and Ellenberg 1974). In addition, the environment of each sample plot was described, with emphasis on site features which could be feasibly measured (Brooke *et al.* 1970). In this paper, nomenclature for vascular plants follows Taylor and MacBryde (1977); for bryophytes Ireland *et al.* (1987) and Stotler and Crandall-Stotler (1977); and for lichens Hale and Culberson (1970).

The vegetation classification followed the methods described by Pojar *et al.* (1987). Reciprocal averaging (Gauch 1977) was used to group floristically similar sample plots. The Braun-Blanquet tabular method was used to identify diagnostic combinations of species (including differential[1] and dominant-differential[2] species) that were exclusive[3] for each group of plots (Pojar *et al.* 1987).

Distinguished zonal, climatic climax plant associations were used to define biogeoclimatic subzones, and the distribution of these associations on zonal sites delineated the geographical extent of the subzones. Floristically similar subzones were grouped into zones. Each zone was defined by a plant order circumscribing all zonal plant associations in that zone. Nomenclature of zones followed Krajina (1965 *et seq.*); subzones were named by adding two or three adjectives indicative of regional climate or vegetation physiognomy (see Table 1).

To examine floristic relationships among the biogeoclimatic zones and subzones, the vegetation data were submitted to principal components analyses (PCAs). PCA, using a reduced number of plots and mid-point percent cover of diagnostic species (see footnote 3 in Table 2), was performed on a correlation matrix (Noy-Meir and Whittaker 1977). The plot reduction, due to our concern of over large variation in sample size, was done randomly to a maximum of 50 plots per biogeoclimatic subzone (zonal plant association). Thus from a total number of 1299 only 633 plots were submitted to PCA. The selective species reduction to diagnostic species (Tables 2 and 4) were shown by Klinka *et al.* (1985) and Courtin *et al.* (1989) to account for the greatest variability in vegetation data.

Overall eigenstructure and significance of axes extracted by PCA were evaluated by tests of variable independence and equicorrelation (Morrison 1976). Relationships between the principal components and vegetation was examined by correlating component scores with individual species values ['component correlation,' Pimentel (1979)]. To avoid cluttering the PCA ordination with a large number of plots, zones and subzones were represented by centroids and 95% confidence ellipses of the first two PCA axis scores (Owen and Chmielewski 1985). Location, orientation, and overlap of confidence ellipses in the two-dimensional space were used to assess affinities among and variability within zones and subzones.

Climate is used in zonal classification only as an accessory characteristic. Each recognized biogeoclimatic unit was climatically characterized, using selected climatic parameters (Trewartha 1968), to assure its ecological significance, i.e., to show correspondence between zonal climax ecosystems and climate. Climatic data were obtained from short- and long-term stations operated by the Atmospheric Environmental Service, Environment Canada (Anonymous 1982), and short-term stations in the network of the Waste Management Branch, B.C. Ministry of Environment. Due to the poor representation of montane, subalpine, and alpine climates, predictions were made for areas outside the networks using isorhythmic maps compiled by the Waste Management Branch or parameter-elevation relationships. The latter involved extrapolating climatic data from selected base stations to predict values at certain elevations where climatic stations are non-existent, as in alpine and some montane and subalpine areas.

Results and Discussion

Biogeoclimatic Zones

When compared to Krajina (1959), the revision conserved all four coastal zones (Table 1), which are well segregated floristically (Table 2). The CDF and CWH zones are differentiated from other zones by the presence of *Thuja plicata* and *Vaccinium parvifolium. Abies grandis, Holodiscus discolor, Mahonia nervosa, Rosa gymnocarpa, Rubus ursinus,* and *Trientalis latifolia* are the prominent differential species for the CDF zone, *Tsuga heterophylla* for the CWH zone, *Tsuga mertensiana* for the MH zone, and *Cassiope mertensiana, Phyllodoce empetriformis,* and *Luetkea pectinata* for the AT zone.

Series in habitat type classification represent aggregations of plant associations, which in practice in the western United States represent groupings of plant associations with the same dominant climax tree species (Pfister and Arno 1980, Franklin *et al.* 1988). A 'habitat type' zone is the land area where a single series is dominant under stable or climax conditions (Franklin *et al.* 1988, p. 30); i.e., the land area with the same dominant climax tree species. According to this system, zones recognized in the coastal forests of western North America include the *Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata, Picea sitchensis, Abies amabilis, Abies lasiocarpa, Chamaecyparis nootkatensis,* and *Tsuga mertensiana* zones. These

TABLE 2. Diagnostic combinations of species for zones of coastal British Columbia.

Column identification		CDF		CWH		MH		AT	
Number of plots		83		1009		187		20	
Biogeoclimatic zone and species	Diagnostic value[1]	Presence class[2] and mean species significance[3]							
CDF and CWH zones									
Thuja plicata	(d)	IV	5	IV	5	I	1		
Vaccinium parvifolium	(d)	IV	2	IV	3	II	1		
Coastal Douglas-fir (CDF) zone and Moist Maritime CDF (CDFmm) subzone									
Abies grandis	(d)	IV	5	I	+				
Acer macrophyllum	(d)	III	3	I	+				
Achlys triphylla	(d)	III	3	I	1	I	+		
Cornus nuttallii	(d)	III	3	I	+				
Festuca subulata	(d)	IV	1	I	+				
Gaultheria shallon	(d,cd)	V	6	II	5	I	+		
Holodiscus discolor	(d)	IV	5	I	+				
Lonicera ciliosa	(d)	IV	1	I	+				
Mahonia nervosa	(d,cd)	V	7	I	2				
Polystichum munitum	(d)	IV	2	II	1	I	+		
Pseudotsuga menziesii	(d,cd)	V	8	III	5	I	+		
Pteridium aquilinum	(d)	IV	3	I	1	I	+		
Rosa gymnocarpa	(d,c)	V	2	I	+				
Rubus ursinus	(d,c)	V	3	I	+				
Kindbergia oregana	(d,cd)	V	6	II	3	I	+		
Symphoricarpos albus	(d)	III	2	I	+				
Symphoricarpos hesperius	(d)	III	4	I	+				
Trientalis latifolia	(d,c)	V	3	I	+				
Coastal Western Hemlock (CWH) zone									
Hylocomium splendens	(d,cd)	III	4	V	5	III	3		
Tsuga heterophylla	(d,cd)	I	2	V	7	III	4		
Mountain Hemlock (MH) zone									
Coptis aspleniifolia	(d)			I	+	III	1		
Rubus pedatus	(d)			II	2	IV	2		
Tsuga mertensiana	(d,cd)			I	2	V	6	II	2
Vaccinium ovalifolium	(d)			II	3	IV	3		
Alpine Tundra (AT) zone and Maritime AT (ATm) subzone									
Barbilophozia floerkei	(d)			I	+	I	1	III	4
Cassiope mertensiana	(d,cd)					II	3	V	7
Luetkea pectinata	(d)					II	2	IV	3
Lycopodium sitchense	(d)					I	+	III	3
Phyllodoce empetriformis	(d,cd)			I	+	II	4	V	7
Rhacomitrium heterostichum	(d)			I	+	I	+	III	3
Vahlodea atropurpurea	(d)					I	+	III	1

[1]Species diagnostic values: d—differential, dd—dominant differential, cd—constant dominant, c—constant (Pojar *et al.* 1987).
[2]Presence classes as percent of frequency: I = 1-20, II = 21-40, III = 41-60, IV = 61-80, V = 81-100.
[3]Species significance class midpoint percent cover and range: + = 0.2 (0.1-0.3), 1 = 0.7 (0.4-1.0), 2 = 1.6 (1.1-2.1), 3 = 3.6 (2.2-5.0), 4 = 7.5 (5.1-10.0), 5 = 15.0 (10.1-20.0), 6 = 26.5 (20.1-33.0), 7 = 41.5 (33.1-50.0), 8 = 60.0 (50.1-70.0), 9 = 85.0 (70.1-100).

zones correspond only roughly to biogeoclimatic zones (Table 1), which represent land areas on which climatic climax vegetation (vegetation of zonal sites) is closely related—but does not necessarily have the same dominant climax tree species.

The first two PCA axes accounted for 41% of the total variance, and all 28 diagnostic species (Table 2) were found to be significantly correlated with the first, or second, or both PCA axes. The species diagnostic for the CDF zone were most strongly and positively correlated with the first axis, whereas the species diagnostic for the AT were most strongly and positively correlated with the second axis. The species diagnostic for the MH and CWH zones were most strongly and negatively correlated with the first and second axis, respectively.

The 95% confidence ellipses obtained from the PCA ordination of 633 sample plots showed that the CDF zone was almost completely separated from the CWH, MH, and AT zones along the first PCA axis; along the second PCA axis the AT zone was almost completely separated from the MH and CWH zones but the MH and CWH zones overlapped (Figure 2). Considering the joint distribution of species and zones (Table 2) and climatic characteristics (Table 3), the first PCA axis represents a precipitation gradient (by isolating the driest CDF zone), and the second PCA axis a temperature gradient. These results can be interpreted as

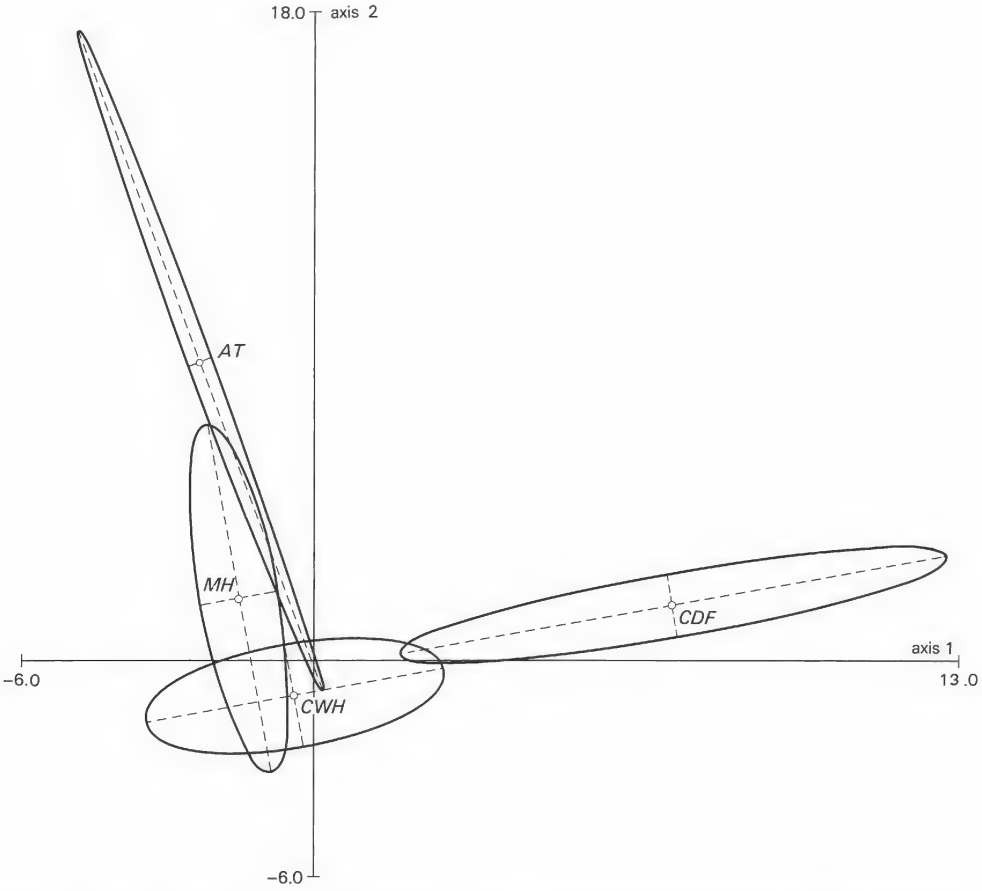

Figure 2. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the AT, MH, CDF, and CWH zones.

TABLE 3. Means and standard deviations (in parentheses) of selected climatic characteristics for AT, MH, CDF, and CWH zones.

Climatic characteristic	CDF	CWH	MH[1]	AT[1]
Number of stations for precipitation data	112	169	47	7
Mean annual precipitation (mm)	1233 (368)	2228 (713)	2620 (578)	2706 (555)
Mean precipitation April-Sept. (mm)	289 (98)	611 (227)	632 (114)	647 (65)
Mean ppt. of the driest summer month (mm)	30 (12)	63 (24)	62 (13)	70 (8)
Mean ppt. of the wettest winter month (mm)	210 (64)	350 (108)	414 (107)	434 (110)
Number of stations for temperature data	73	11	47	17
Mean annual temperature (°C)	9.6 (0.5)	7.9 (1.6)	3.0 (1.1)	0.3 (0.9)
Mean temperature of the warmest month (°C)	17.0 (0.8)	15.6 (1.7)	11.1 (1.1)	9.2 (0.8)
Mean temperature of the coldest month (°C)	2.3 (1.0)	0.2 (3.0)	−5.1 (1.7)	−8.9 (2.7)
Number of months with mean temperature > 10°C	5.5 (0.5)	4.7 (0.8)	1.7 (0.9)	0.1 (0.4)
Index of continentality[2]	12 (3)	13 (7)	16 (3)	20 (7)

[1]All values given for the AT and MH zones were extrapolated from selected base stations in the CWH zone.

[2]Index of continentality = $[1.7(\text{mean } T_{JULY} - \text{mean } T_{JAN})/\sin_{DEGREES\ LATITUDE}] - 20.4$, where T−temperature (°C) (after Rose and Grant 1976).

demonstrating that the CDF zone is a discrete regional ecosystem, while the AT, MH, and CWH zones represent floristically-defined segments of an altitudinal climatic gradient.

In the Pacific Northwest, the same gradients have been interpreted or identified as the primary environmental gradients underlying the variation in zonal vegetation (e.g., Franklin and Dyrness 1973, Dyrness *et al.* 1974, Zobel *et al.* 1976, del Moral and Watson 1978, Agee and Kertis 1987). Temperature appears to be more important in separating between vegetation zones, whereas moisture tends to be more useful in differentiating within submontane and montane zones (Zobel *et al.* 1976). The array of zonal climax plant associations in the two-factor ordination in Figure 2 generally corresponds to the ordinations presented by Zobel *et al.* (1976, Figure 7) and Agee and Kertis (1987, Figure 2).

From the suite of available climatic characteristics, we choose to emphasize the differences in temperature and precipitation, with temperature-related variables appearing to best summarize the differences among the zones (Table 3). Precipitation-related variables segregated the CDF zone from the CWH zone—the former associated with a dry cool mesothermal (Csb) climate, the latter with a wet cool mesothermal (Cfb) climate (Trewartha 1968). At approximately 10°C, mean annual range of temperature (i.e., the mean temperature of the warmest month minus that of the coldest month) in the CDF and CWH zones is the smallest for regional climates in Canada (Schaefer 1978). Mean annual temperatures in the CDF zone are among the highest in Canada, and heavy precipitation makes the CWH and MH zones and Maritime AT subzone by far the wettest part of Canada.

The CDF, CWH, MH, and AT zones manifest abrupt vegetation changes that occur in response to abrupt climatic changes in coastal mountains. At elevations above approximately 1500 m, scattered clumps of trees give way to krummholz, low shrub, and heath (dwarf evergreen shrub) communities under the influence of alpine tundra (ET) climate. Below 1500 m and above approximately 1000 m and with decreasing elevation, scattered clumps of trees merge with more continuous forest under the influence of maritime subalpine boreal (Dfc) climate with deep snow cover. Heavy snowpacks insulate MH soils from frost. The MH zone

is the core distributional area of *Tsuga mertensiana*. Snow depth in the AT zone is generally less than in the MH zone. Lower temperatures, however, retard the melting rate of snow in alpine ecosystems so that snow duration critically influences alpine vegetation. When the subalpine climate becomes more continental and soils freeze before deep snow accumulates, *Tsuga mertensiana* and *Abies amabilis* are replaced by *Picea engelmannii* and *Abies lasiocarpa*, and the MH zone is replaced by the Engelmann Spruce–Subalpine Fir (ESSF) zone.

Snow depth and duration have less influence on the vegetation at elevations below approximately 1000 m (Brooke *et al.* 1970). These lower elevations feature a wet cool mesothermal (Cfb) climate which coincides with the core distributional area of coastal *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*. *Tsuga heterophylla* is nearly absent in the CDF zone, with the mean precipitation of the driest month of summer ≤ 30 mm, whereas in the CWH zone, with a mean precipitation of the driest month of summer >30 mm, this shade-tolerant species has the potential to dominate the tree stratum on zonal sites. Inland from the core distributional area of *Tsuga heterophylla*, with increasing continentality and decreasing temperature and/or precipitation, the CWH zone is replaced by interior or continental biogeoclimatic zones east of the Coast-Cascade Mountains.

Coastal Douglas-fir Subzone

We have retained only one subzone–the Moist Maritime CDF (CDFmm) subzone (formerly the Drier CDF subzone)–within the CDF zone and amalgamated the former Wetter CDF subzone and the Vancouver Island portion of the former Drier CWH subzone into a Very Dry Maritime CWH (CWHxm) subzone (Table 1). A comparison of these latter two units showed high floristic similarities (exemplified by widespread occurrence of *Rhytidiadelphus loreus* and *Tsuga heterophylla*) and climatic similarities (a relatively uniform, wet cool mesothermal climate) (see Table 4); the original Drier CDF subzone, however, has distinct zonal vegetation (Table 2), and a dry cool mesothermal climate (Table 3). The diagnosis of the CDFmm subzone is based on 82 samples from the Saanich Peninsula (Roemer 1972), which

TABLE 4. Means and standard deviations (in parentheses) of selected climatic characteristics for CWH subzones[1].

Characteristic	CWHwh	CWHvh	CWHxm	CWHdm	CWHmm	CWHwm	CWHvm	CWHds	CWHms	CWHws
Number of stations for precipitation data	5	28	81	53	13	6	34	9	5	4
Mean annual precipitation (mm)	1349 (146)	2951 (657)	1505 (385)	1827 (326)	2349 (453)	2124 (342)	2787 (680)	1627 (367)	1683 (312)	1449 (410)
Mean precipitation April-Sept. (mm)	433 (61)	890 (193)	363 (96)	498 (89)	470 (50)	780 (242)	752 (200)	419 (109)	423 (90)	412 (148)
Mean ppt. of the driest summer month (mm)	54 (10)	96 (22)	39 (13)	53 (10)	45 (5)	86 (29)	75 (21)	45 (11)	40 (4)	45 (18)
Mean ppt. of the wettest winter month (mm)	204 (21)	431 (113)	251 (70)	292 (55)	400 (75)	362 (44)	436 (103)	259 (54)	262 (48)	244 (64)
Number of stations for temperature data	5	21	54	53	13	6	21	7	3	4
Mean annual temperature (°C)	7.6 (0.2)	8.2 (0.9)	9.3 (0.6)	9.8 (0.4)	5.7 (0.9)	5.5 (0.3)	8.2 (1.1)	7.8 (1.2)	5.9 (0.8)	5.5 (0.8)
Mean temperature of the warmest month (°C)	14.6 (0.3)	13.9 (0.8)	17.0 (0.8)	17.6 (0.5)	14.1 (1.0)	14.1 (0.8)	16.0 (1.1)	17.4 (1.4)	15.1 (0.8)	15.5 (1.0)
Mean temperature of the coldest month (°C)	1.3 (0.6)	3.0 (1.4)	1.8 (0.9)	1.9 (0.7)	−2.2 (1.1)	−4.2 (1.3)	0.3 (2.7)	−3.0 (2.3)	−4.2 (0.8)	−6.0 (0.6)
Number of months with mean temp. >10°C	4.0 (0.0)	4.4 (0.7)	5.4 (0.5)	5.7 (0.4)	3.9 (0.5)	3.8 (0.4)	4.9 (0.6)	5.0 (0.6)	4.3 (0.6)	4.2 (0.5)
Index of continentality	6 (2)	3 (2)	14 (3)	15 (2)	16 (2)	17 (4)	14 (6)	24 (7)	23 (0)	24 (3)

[1]Symbols for CWH subzones are defined in Table 1.

form the zonal *Pseudotsuga-Mahonia* plant association.

This revision restricts the CDF zone to the driest part of Vancouver Island, the Gulf Islands, and the southern mainland coast, in the rain shadow of the Olympic and Vancouver Island Mountains; i.e., to the area where coastal Douglas-fir is a moderately shade-tolerant tree and has the potential to dominate the tree stratum on zonal sites. This area extends south through Washington (in the Puget Sound rain shadow of the Olympic Mountains) and Oregon (Willamette Valley and Umpqua and Rogue Valleys) (Franklin and Dyrness 1973). If our sampling, classification, and analysis included the entire area influenced by a dry cool mesothermal climate, more CDF subzones would likely be recognized in response to floristic and climatic variations along a latitudinal gradient.

Coastal Western Hemlock Subzones

Our initial tabular analysis of CWH subzones failed to differentiate each zonal plant association (subzone) from the others, except at the climatic extremes of the data set. The analysis suggested that the differentiation could be more successful and clearer vegetation-climate relationships could be shown if subzones were subset into more inclusive groups. Therefore, we interpolated two categories between subzone and zone categories.

The two intercalary categories helped differentiate ten zonal plant associations, each delineating a subzone (tabular data available from the authors on request). All these associations belong to the *Tsuga heterophylla-Rhytidiadelphus loreus* plant order. The ten proposed CWH subzones [compared to the former drier and wetter subzones (Krajina 1965)] resulted from a combination of the three continentality strata (hypermaritime, maritime, and submaritime strata or subzones) and five relative precipitation strata [very dry, dry (drier stratum or subzones) and moist, wet, and very wet (wetter stratum or subzones)]. The first (more-inclusive) intercalary category related subzones to the three continentality strata, and the second (less-inclusive) category related subzones to two general precipitation strata (drier and wetter).

This large increase in the number of proposed CWH subzones can be explained by the large increase in the data base. The former drier and wetter subzones were based on data obtained only from the southern maritime portion of the CWH zone. We now have a fairly complete sampling over the broad range of floristic and climatic variation included in the CWH, our largest coastal zone.

Maritime subzones that represent the central concept of the CWH zone are without diagnostic species, which is permissible for one unit in relation to other units of the same rank and circumscription (Pojar *et al.* 1987). *Blechnum spicant, Coptis aspleniifolia, Listera cordata, Rhizomnium glabrescens, Picea sitchensis,* and *Scapania bolanderi* are diagnostic species for hypermaritime subzones; *Clintonia uniflora, Orthilia secunda,* and *Pleurozium schreberi* are diagnostic species for submaritime subzones.

Within each continentality stratum, a diagnostic combination of species was identified for each precipitation stratum. For example, within the maritime and submaritime strata, the wetter (moist to wet or very wet) subzones are segregated from the drier (very dry to dry) subzones by a prominent presence of *Abies amabilis, Cornus canadensis, Vaccinium alaskaense,* and *V. ovalifolium. Pseudotsuga menziesii* is the only diagnostic species common to the drier subzones. With the exception of *Gaultheria shallon,* differences between the Wet and Very Wet Hypermaritime CWH subzone are not strong (essentially showing trends in significance of diagnostic species); similar differences are apparent for wetter submaritime subzones (tabular data available from the authors on request).

The first two PCA axes accounted for 28% of the total variance, and all 43 diagnostic species were significantly correlated with the first, the second, or both PCA axes. The species diagnostic for the drier subzones were negatively correlated with the first axis, whereas the species diagnostic for the wetter subzones were postively correlated. This suggests that the greatest proportion of variance in species significance coincides with precipitation, and that the CWH subzones are primarily separated by precipitation (Dyrness *et al.* 1974, Zobel *et al.* 1976). The second axis appeared to be related to a temperature (continentality) gradient.

The PCA ordination of CWH sample plots was further examined by calculating 95% confidence ellipses for the three continentality and two precipitation strata and the subzones within each continentality stratum. The locations of the three continentality strata in the ordination indicated that the maritime subzones encompass most of the variation in the data set while the hypermaritime and submaritime subzones refer to specific regions within the total variation (Figure 3). Within the

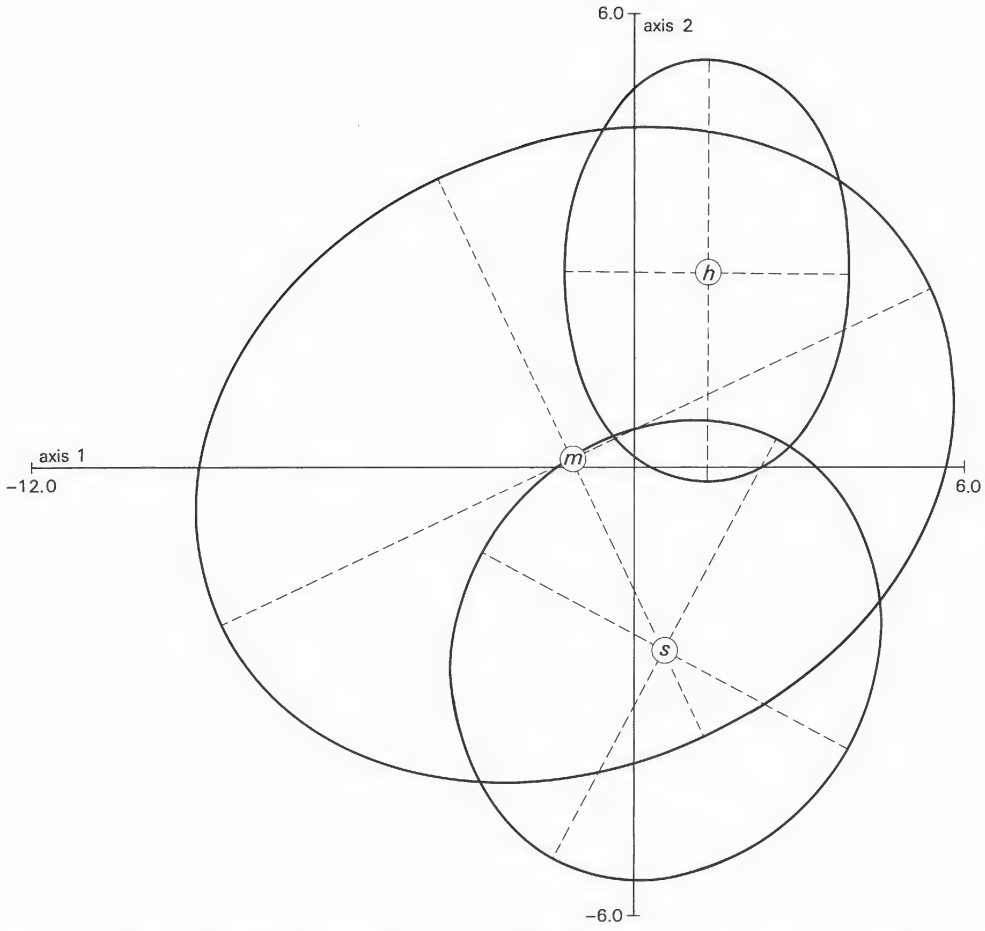

Figure 3. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the hypermaritime (h), maritime (m), and submaritime (s) CWH subzones.

hypermaritime stratum, the confidence ellipses for the wet and very wet subzones nearly completely overlapped. Within the maritime stratum the very dry, dry, and moist subzones were distinct from the wet and very wet subzones, which showed a nearly complete overlap (Figure 4). Within the submaritime stratum, all three subzones appeared to form distinct groups.

Climatic data compiled for continentality strata manifest decreasing precipitation (most apparent in the mean precipitation data of the wettest winter month), decreasing temperature of the coldest month, and increasing index of continentality along the longitudinal gradient (Table 4). Furthermore, marked differences between the drier and wetter precipitation strata in both precipitation and temperature related parameters are evident in the climatic summary.

There are pronounced differences in precipitation between the wet and the very wet hypermaritime subzones (Table 4). The former is located on the leeward side of the Queen Charlotte Islands, the latter occurs on the windward side of the Queen Charlotte Islands, the outer central mainland coast, and the outer west coast of Vancouver Island. In relative terms, the wet hypermaritime subzone is

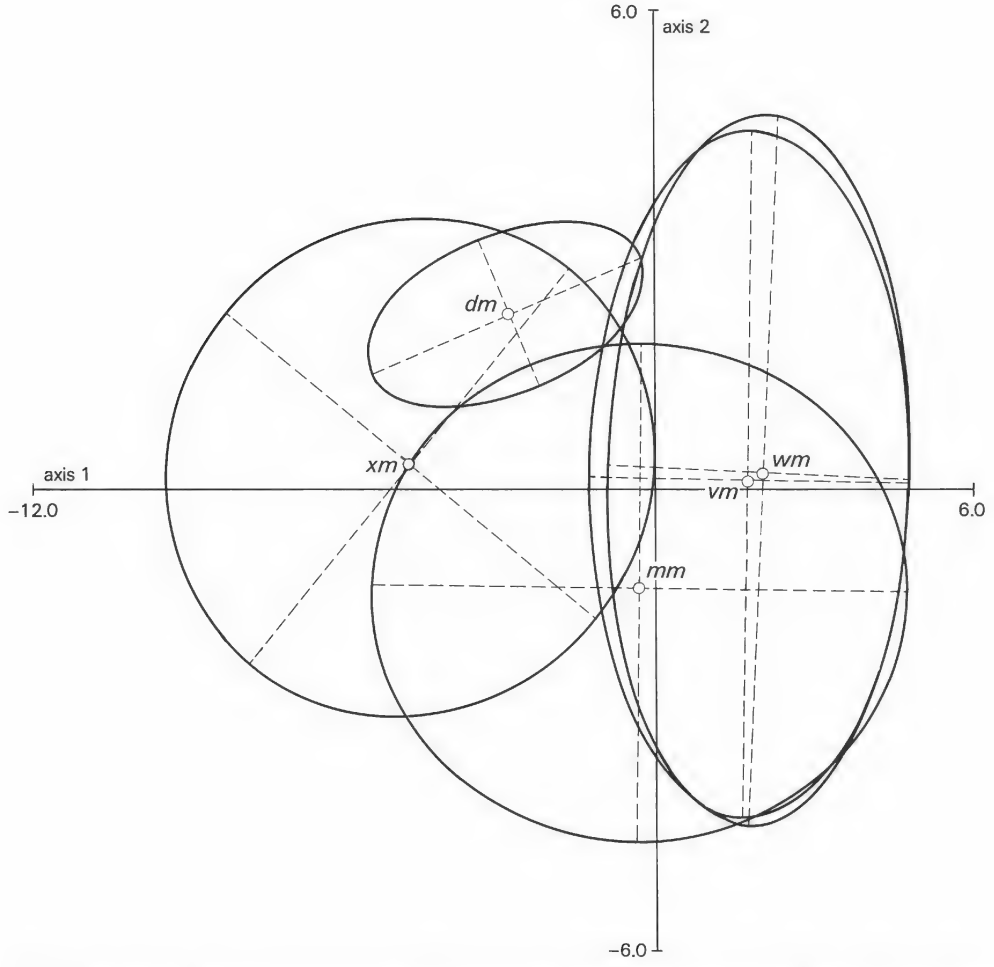

Figure 4. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the very dry maritime (xm), dry maritime (dm), moist maritime (mm), wet maritime (wm), and very wet maritime (vm) CWH subzones.

drier and cooler than the very wet hypermaritime subzone. Rainy and cloudy summer, wet fall, rainy winter with relatively low snowfall and ephemeral snowpack, and equable temperature are the characteristic climatic features of the hypermaritime subzones.

The very dry and dry maritime subzones are drier and warmer than the other maritime subzones (Table 4). The low growing-season precipitation of the moist maritime subzone (located on the windward side of Vancouver Island) and the cool winter temperature of the wet maritime subzone (located on the northern coastal mainland) segregate them from the very wet maritime subzone. Considering the mean temperature of the coldest month, the moist and the wet maritime subzones appear to have a wet cool temperate climate (Dfb) which is suggestive of an ecotone between the wet cool mesothermal and montane or subalpine boreal climates.

Submaritime subzones differed from each other mainly in temperature characteristics—the dry subzone being warmer than the moist and the wet subzones (Table 4). The wet submaritime subzone,

located at higher latitudes, is the coolest in winter. All submaritime subzones also appear to have a wet cool temperate climate. Considering indices of continentality, the submaritime belt (see Figure 1) is likely dominated by a mild cool temperate climate.

As latitude increases, temperature decreases and the rain shadow of the Vancouver Island Ranges disappears—this is recognized in the presence of the 'cooler' wet maritime and wet submaritime subzones (Table 4) and the absence of drier subzones along the central and northern coast. Climatic changes along the longitudinal gradient are complicated by the presence of two successive large-scale mountain barriers aligned in a northwest to southeast direction—Queen Charlotte Island Mountains/Vancouver Island Ranges and Coast Mountains. When the air is forced up the west-facing slopes of these mountains, weather systems carried by prevailing westerly winds aloft drop considerable moisture; on the eastern slopes, the air descends and is heated by compression, causing the clouds to dissipate (Schaefer 1978). As a result, the windward slopes are always wetter and the leeward slopes are always drier and become more continental with increasing distance from the Pacific Ocean. Thus, drier subzones, with a prominent component of *Pseudotsuga menziesii*, are located at low elevations on the leeward side of coastal mountains (the very dry and dry maritime subzones in the rain shadow of the Olympic Mountains and Vancouver Island Ranges; and the dry submaritime subzone in the rain shadow of the Coast Mountains).

Wetter subzones, with a prominent component of *Picea sitchensis* or *Abies amabilis*, are located on the leeward side of the Queen Charlotte Mountains (the wet hypermaritime subzone) and Vancouver Island Ranges (the moist maritime subzone) and are drier and somewhat continental compared to their windward counterpart (Table 5).

Mountain Hemlock Subzones

By interpolating a category between the zone and subzone categories, it was possible to segregate four zonal plant associations corresponding to four subzones [compared to the former parkland and forested subzones (Krajina 1965)] (Tables 1 and 5). All four associations belong to the *Tsuga mertensiana* plant order. Relationships between subzones and continentality of a subalpine boreal climate were inferred from the continentality strata characterized for a cool mesothermal climate (CWH zone). This, however, cannot be confirmed without on-site climatic data (extrapolation of data from submontane stations was avoided).

Attempts to differentiate between maritime and submaritime subalpine strata showed primarily an increase in the presence and cover of *Abies lasiocarpa* and a decrease in *Chamaecyparis nootkatensis*. As a result, four proposed MH subzones were formed by a combination of merely two continentality strata (hypermaritime and maritime) and two physiognomic strata (parkland and forested) (Table 5). Minor floristic variations along the longitudinal gradient, presumably reflecting variations in continentality, were used to distinguish windward (more maritime) and leeward (less maritime) variants for each of the four subzones. It may be that in zonal climax vegetation the floristic contrast (and perhaps the climatic contrast) between maritime and submaritime strata diminishes with increasing altitude, or it may be that our present data base does not adequately represent the submaritime stratum of the MH zone. The recognition of additional subzones again reflects expanded sampling throughout the range of the zone. The former parkland and forested subzones were based on samples from the southern maritime portion of the MH zone.

The differentiation of MH subzones is not very strong, probably reflecting a low sampling intensity, especially in parkland subzones (Table 5). Hypermaritime subzones are distinguished by the nearly constant presence of *Blechnum spicant, Chamaecyparis nootkatensis, Coptis aspleniifolia, Hylocomium splendens, Picea sitchensis, Rhytidiadelphus loreus*, and *Tsuga heterophylla*—species that occur mainly within wet cool mesothermal climates. Maritime subzones, which represent the central concept of the MH zone, are differentiated by *Abies amabilis* and *Vaccinium membranaceum*, the latter species more typical of continental boreal climates.

In addition to the physiognomic differences (discontinuous versus continuous forest cover), diagnostic combinations of species for the parkland subzones include alpine elements, such as *Phyllodoce* spp. and *Cassiope* spp., while the intermediate presence of *Tsuga heterophylla* is characteristic for the lower portion of forested subzones (Table 5). The lack of differential species for the parkland hypermaritime subzone is attributed to inconsistencies in the nine samples collected on the Queen Charlotte Islands.

TABLE 5. Diagnostic combinations of species for subzones of the Mountain Hemlock (MH) zone.

Column identification		MHph		MHfh		MHpm		MHfm	
Number of plots		9		31		25		122	
Biogeoclimatic zone and species	Diagnostic value	Presence class and mean species significance							
Hypermaritime MH (MHh) subzones									
Blechnum spicant	(d)	IV	1	V	2			I	+
Chamaecyparis nootkatensis	(d)	IV	5	IV	6	II	2	II	3
Coptis aspleniifolia	(d,c)	IV	1	V	2			I	+
Cornus canadensis	(d)	III	2	IV	1			II	1
Hylocomium splendens	(d)	IV	4	V	4			II	2
Plagiothecium undulatum	(d)	III	1	IV	2			I	+
Rhytidiadelphus loreus	(d,cd)	V	5	V	6			III	3
Parkland Hypermaritime MH (MHph) subzone									
Cladina rangiferina	(d)	III	2			I	1	I	+
Phyllodoce empetriformis	(d)	III	5			V	5	I	1
Forested Hypermaritime MH (MHfh) subzone									
Calamagrostis nutkaensis	(d)	I	2	III	3				
Huperzia selago	(d)	I	+	IV	1			I	+
Listera caurina	(d)			III	1			I	+
Listera cordata	(d,c)	II	+	V	2	I	+	I	+
Menziesia ferruginea	(d)	I	+	III	2	I	+	IV	3
Mnium glabrescens	(d)	I	+	III	3			I	1
Moneses uniflora	(d)	I	+	III	1	I	+	I	+
Pellia neesiana	(d)	I	1	III	2				
Picea sitchensis	(d)	I	2	IV	4			I	+
Scapania bolanderi	(d,c)	II	3	V	4			I	+
Sphagnum girgensohnii	(d)	I	2	III	3			I	1
Streptopus roseus	(d)	II	+	IV	2	I	+	II	2
Tsuga heterophylla	(d,cd)	III	2	V	5	I	3	III	4
Vaccinium parvifolium	(d)	I	1	IV	2			I	+
Maritime MH (MHm) subzones									
Abies amabilis	(d,cd)	II	2	I	1	IV	4	V	6
Vaccinium membranaceum	(d)					V	5	IV	4
Parkland Maritime MH (MHpm) subzone									
Abies lasiocarpa	(d)			I	+	IV	4	II	3
Cassiope mertensiana	(d,cd)	II	2	I	2	V	5	I	+
Luetkea pectinata	(d)	II	2	I	+	IV	3	I	1
Phyllodoce empetriformis	(d,cd)	III	5			V	5	I	1
Vaccinium deliciosum	(d)	I	1			III	3	I	+
Forested Maritime MH (MHfm) subzone									
Menziesia ferruginea	(d)	I	+	III	2	I	+	IV	3
Rhytidiopsis robusta	(d,cd)	II	1	III	4	III	3	V	6
Rubus pedatus	(d,c)	IV	1	IV	2	III	1	V	4
Tsuga heterophylla	(d)	III	2	V	5	I	3	III	4
Vaccinium alaskaense	(d)	IV	3	III	4	I	2	IV	5

Diagnostic values, presence class, and mean species significance are defined in Table 2.

The first two PCA axes accounted for 45 percent of the total variance and all 24 diagnostic species (Table 5) were found to be significantly correlated with the first, the second, or both PCA axes. The species diagnostic for the hypermaritime subzones were correlated positively with the first axis, whereas the species diagnostic for the parkland and forested maritime subzones were correlated negatively. This suggests that the first axis reveals contrasts in continentality. The second axis appears to be related to a temperature gradient.

The PCA ordination of MH sample plots using 95% confidence ellipses for the four subzones complements the correlation pattern described for diagnostic species (Figure 5). The overlap of the confidence ellipses for the parkland and forested subzones indicates a gradual floristic change along an altitudinal gradient in the MH zone.

Scattered tree cover and persistent snowpack are the most obvious characteristics of parkland subzones. Trees grow largely on organic mounds that are free of snow for more than approximately

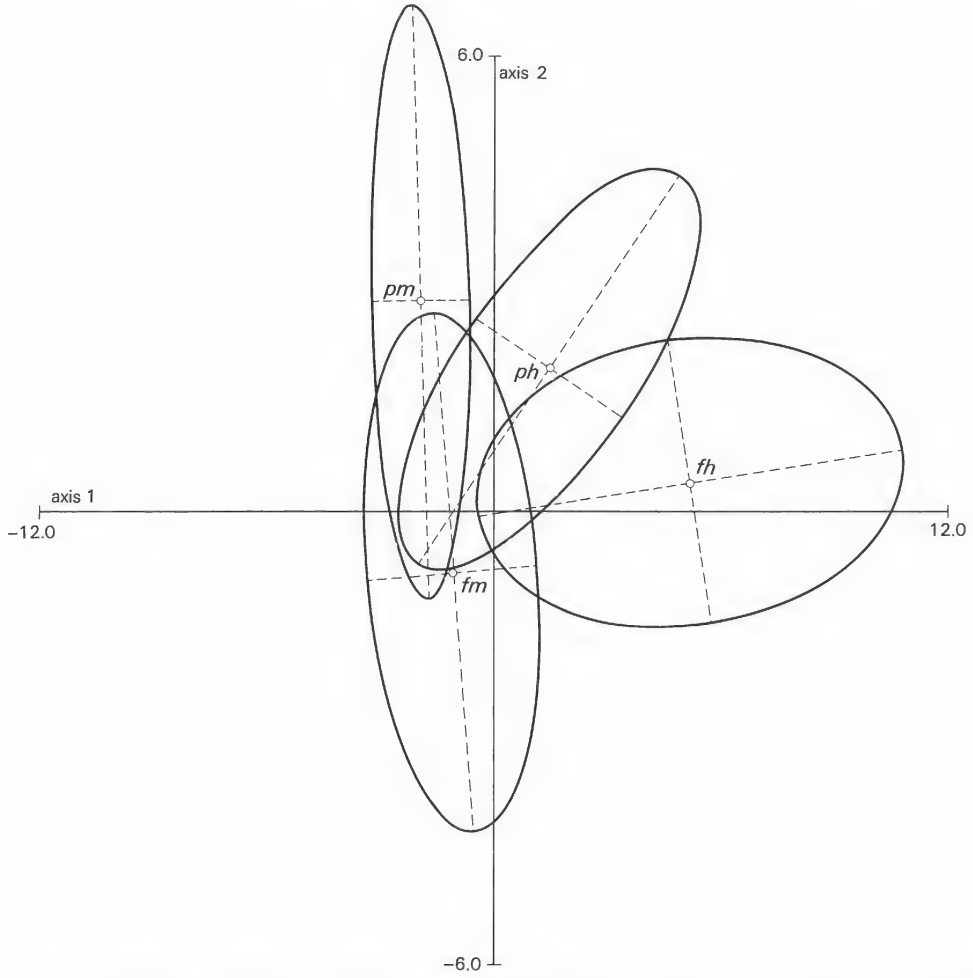

Figure 5. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the parkland, hypermaritime (ph), forested hypermaritime (fh), parkland maritime (pm), and forested maritime (fm) MH subzones.

three months. Heath, low shrub, graminoid, or forb communities influenced by more persistent snowpack cover much of the remaining area of parkland subzones. In contrast, forest cover is largely continuous in forested subzones and the climate is slightly warmer. Snow depth and duration are less than in the parkland subzones, resulting in a longer growing season and the establishment of complex forest communities (Brooke *et al.* 1970).

Alpine Tundra Subzone

There are insufficient data to differentiate the coastal portion of the AT zone beyond one subzone—the Maritime AT (ATm) subzone (Tables 1 and 2). This subzone is diagnosed by 40 samples that form the zonal *Cassiope-Phyllodoce* plant association (Archer 1963) in the southern portion of the Pacific Ranges. Field observations, however, indicate that the changes in zonal alpine communities along the longitudinal gradient parallel those described in this paper for zonal subalpine communities.

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Footnotes

1. Differential species are clearly associated with one or more than one unit in a hierarchy; presence class $\geq$III and at least two presence classes greater than in other units of the same category and circumscription.

2. Dominant-differential species do not meet the presence criteria above but show clear dominance in one or more than one unit in a hierarchy; presence class $\geq$III, mean species significance $\geq$5 and two or more significance classes greater than in other units of the same category and circumscription.

3. A unit is distinguished by an exclusive diagnostic combination of species that must include at least one differential or dominant-differential species; the unit that represents the central concept of a higher circumscribing unit can also be recognized without a diagnostic combination of species.

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Development of Dwarf Mistletoe Infections on Inoculated Western Hemlock Trees in Southeast Alaska

Abstract

In the autumn of 1977, 1978, and 1979, mature seeds of hemlock dwarf mistletoe (*Arceuthobium tsugense*) were placed on needles and twigs of young western hemlock trees growing on a clearcut in Juneau, Alaska to provide information on seed retention and germination, infection development and survival, and generation time. Retention over one winter of 1,956 placed seeds averaged 65 percent while germination of retained seeds was 33 percent. Two hundred and sixty infections developed, 78 percent of which produced dwarf mistletoe shoots; however, over the 11 to 12 years that infections were observed, no seeds were produced and shoots were frequently broken or damaged. Plant damage, branch death, pollination biology, and environmental conditions are discussed as possible reasons for the lack of seed production and failure to complete the life cycle. Comparisons are made to other inoculation studies with *A. tsugense*. These comparisons indicate that the initial process of infection development, after mistletoe seeds are captured on needles or twigs, does not appear to account for the markedly lower infection levels that have been noted between stands in southeast Alaska and those further south.

Introduction

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) is widespread in old-growth stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in southeast Alaska (Laurent 1974). The disease is, however, regarded as less of a problem in managed, young stands of western hemlock in southeast Alaska than in similar stands farther south in coastal British Columbia, Washington, or Oregon (Shaw 1982, Hennon and Shaw 1988, Shaw and Hennon 1991). There are several hypotheses as to why this difference exists (Drummond and Hawksworth 1979, Shaw 1982, Shaw and Hennon 1990). A primary reason appears to be that spread and intensification of dwarf mistletoe in infested stands, even beneath infected residual trees where young hemlocks are highly prone to infection (Shaw 1982, Shaw and Hennon 1991), is markedly lower in southeast Alaska than in similar stands elsewhere.

Why fewer infections are present in these stands than in similar stands in coastal British Columbia, Washington, or Oregon is unknown, but many possibilities exist. For example, there may be differences in pollination biology, seed production, seed viability, seed dispersal, seed retention, seed germination, infection development, infection survival, or generation time (Hawksworth and Weins 1972). This paper reports results of field inoculation studies designed to provide information on these latter five factors and compare results with those reported from similar studies conducted on *A. tsugense* in other locations.

Methods

Mature seeds of *A. tsugense* were collected from infected western hemlock trees within the City and Borough of Juneau, Alaska in September of 1977, 1978, and 1979. Soon after each year's collection, moistened seeds were placed on foliage and branches of young western hemlock trees growing in the city near Lemon Creek. This dense, unthinned stand of young-growth western hemlock and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) developed after clearcut logging in 1958-60. It is on a gentle, south-facing slope and is rather typical of young stands throughout southeast Alaska (Harris and Farr 1974).

In 1977, 963 seeds were placed on twigs and one-year-old needles in lower and middle crown branches, as follows: 160 on individual needles with a positive angle of attachment to the twig, 160 on individual needles with a negative angle of attachment to the twig, 50 on needles with a near zero (horizontal) angle of attachment to the twig, and 593 directly on twigs (Figure 1). Only one placement type was used per branch. In 1978, 783 seeds were placed: 200 on needles with a

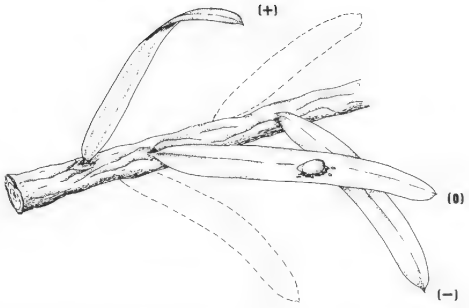

Figure 1. Side view of a western hemlock twig showing positive (+), near horizontal (0), and negative (−) angles of needle attachment. Placement of a dwarf mistletoe seed is shown on the (0) needle.

positive angle of attachment, 163 on needles with a negative angle, 168 on horizontal needles, and 252 directly on twigs. In 1979, 210 seeds were placed on twigs. There was no other source of dwarf mistletoe seed within several hundred meters of the inoculation sites.

All inoculations were examined at irregular intervals every few months during the first 4 years after seed placement and the percentage of seeds retained was calculated for each type of inoculation site after the first winter. Percent germination was calculated for these retained seeds for each year of inoculation. For the needle sites, retention included seeds that moved, primarily via rain droplets, to twigs and needle bases as these sites are the primary infection courts (Roth 1959). Seeds were placed directly on twigs and needles with different orientations to simulate actual interception of seeds ejected from explosive fruits on mature, female infections (Hawksworth and Wiens 1972). Examination of 45, one-year-old needles on each of 10 different lower crown branches (450 total needles) in the study stand showed that 52% had a positive angle of attachment, 28% were horizontal, and 20% had a negative angle of attachment.

Inspections were made approximately biannually after 1983 until 1986 and then annually until 1988. A cursory examination of the 1978 and 1979 inoculations was made in March 1990 to assess shoot production, seed production, and branch mortality. The proportion of retained seeds that developed into infections was determined by noting where branch swellings formed at inoculation sites or wherever the seeds finally rested. The time period for infections to first be detected as noticeable swellings, the temporal pattern of production and retention of dwarf mistletoe shoots and fruits on female shoots, the appearance of witches' brooms (Baranyay *et al.* 1971), and infection mortality also were calculated.

Results

Seed retention and germination

Table 1 shows the proportion of seeds retained after one winter for each inoculation type. Needles with a negative angle of attachment had the lowest level of retention while those with a positive angle of attachment had the highest. Direct twig placements and horizontal needles had intermediate levels of seed retention. The percentage of retained seeds that germinated for the 1977, 1978, and 1979 inoculations was 29 percent, 38 percent, and 25 percent, respectively.

Infection development

By September 1983, 260 infections had developed from the 1,956 seeds placed (1,265 retained) over the 3-year inoculation period (Table 2). Over this period, 147 different branches had been used in the experiments; 65, or 44 percent of these branches were dead by 1986 and only 211 viable infections remained. The 122 branches used for inoculations in 1977 and 1978 were reexamined in 1988; 61 (50%) were dead. Nineteen of the 23 branches inoculated in 1979 were dead in 1990; prior to death, infections had developed on 11 of these branches. By this time, continued tree growth had relegated most inoculated branches to interior portions of the lower crown. Thus, mortality was associated with natural pruning of lower-crown branches through shading, not the development of infections per se.

Most infections readily produced dwarf mistletoe shoots (Table 2); however, regardless of month of examination, these shoots were consistently immature and frequently broken so that only basal cups remained. This constant scarcity of mature shoots precluded accurate sex determination of dwarf mistletoe plants.

Branch swelling, the initial symptom of infection, was generally detectable from 32-35 months after inoculation. The earliest swellings appeared about 24 months after inoculation, but some did not appear for 72 months. For the successful inoculations that produced shoots, the time after seed placement to shoot production for 1977, 1978,

TABLE 1. Retention of dwarf mistletoe seeds in southeast Alaska one winter after inoculation in 1977, 1978, and 1979.

	Type of inoculation site[1]					
year	positive needle angle	negative needle angle	horizontal needle angle	twig	total retention	# of seeds placed
1977	82%	9%	30%	72%	61%	963
1978	87%	16%	43%	83%	62%	783
1979	(all placed on twigs)			92%	92%	210
mean	84%	13%	30%	79%	65%	–
# of seeds placed	360	323	218	1055	–	1956

[1]see Figure 1 for clarification of needle angles

TABLE 2. Development of dwarf mistletoe infections in southeast Alaska by September 1983 for inoculations in 1977, 1978, and 1979.

Year	No. of infections	% of placed seeds that resulted in infection	% of retained seeds that resulted in infection[1]	% of germinated seeds that resulted in infection	% of infections with plants or basal cups
1977	156	16%	27%	92%	72%
1978	81	10%	17%	44%	86%
1979	23	11%	12%	48%	87%
Total	260	13%	21%	65%	78%

[1]retained over one winter

and 1979 inoculations approximated, respectively, 40 months (range 32-72 months), 42 months (range 36-72), and 48 months (range 36-60 months). We did not statistically analyze these apparent annual differences because our irregular times of examination could have accounted for the difference. At no time during the 11-12 years that these infections were examined did any mature seeds develop. Thus, the life cycle was not completed and a generation time could not be calculated.

Individual inoculation points were 5 to 10 cm apart when seeds were originally placed on twigs or needles. Because of seed movement, many infections developed adjacent to each other. Nineteen infections had developed characteristics of incipient witches' brooms by 1986. Although it was difficult to verify conclusively, most of these broomed infections appeared to have developed through the merging of two or more adjacent infections.

Discussion

The 65 percent retention of seeds over the first winter after placement is nearly identical to the 66 percent reported from a comparable study in Oregon that also spanned a 3-year period of inoculation (Carpenter *et al.* 1979). The 92 percent retention for seeds placed on twigs in the 1979 inoculations is similar to the 96 percent observed for twig inoculations in southern British Columbia (Smith 1974). Our overall infection success of 13 percent (260 infections developing from 1,956 placed seeds) was, however, markedly higher than the 5.3 percent that occurred in Oregon. This difference occurred even though the germination success we observed for retained seeds (25-38%) was considerably lower than the 45 percent observed in both Oregon (Carpenter *et al.* 1979) and southern British Columbia (Smith 1974). Germination success in all three of these studies conducted in predominately cool but wet forests were markedly lower than the 67% germination reported for seeds of *A. tsugense* stored *in vitro* for 130 days under dry, cool, and dark conditions (Wicker 1974).

Twenty-one percent of the 1,265 seeds that were retained over one winter developed into infections (Table 2). This frequency compares to 8 percent in Oregon (Carpenter *et al.* 1979) and

18 percent and 22 percent in two studies in southern British Columbia (Smith 1971, 1974). Infection success, based on retained seeds that germinated, was 65 percent in our study (Table 2), but only 17 percent in Oregon (Carpenter *et al.* 1979).

This striking difference may result from use of dissimilar criteria in judging germination, although this seems unlikely since radicle emergence is a generally accepted definition of germination for dwarf mistletoe seeds (Gill 1935, Beckman and Roth 1968) and is relatively easy to ascertain. Another possibility is that some extreme environmental conditions developed at the Oregon inoculation site after germinants had formed, but before they were able to establish infections. This scenario also seems unlikely, however, as the inoculations spanned a 3-year period and the probability of occurrence of such events in 3 successive years is rather low.

We consider the most probable explanation for the difference to be that there was, for unknown reasons, a higher level of germinant mortality in Oregon than in southeast Alaska due primarily to fungal attack and insect predation, common causes of seed loss for dwarf mistletoes (Hawksworth 1961, Wicker 1974, Carpenter *et al.* 1979). At any rate, the process of infection development, after seeds are captured on needles or twigs, does not appear to account for the marked difference in infection levels that has been noted between stands in southeast Alaska and those farther south (Shaw 1982, Shaw and Hennon 1991).

The inoculation studies with *A. tsugense* in Oregon (Carpenter *et al.* 1979) and in southern British Columbia (Smith 1971, 1974) suggest a generation time necessary to complete the life cycle (production of seeds by female plants) of 4 to 5 years. This generation time is typical for species of dwarf mistletoe (*Arceuthobium*) (Hawksworth and Wiens 1972). The time necessary for the Alaskan infections to develop noticeable swellings and produce plants was comparable to that recorded in the above mentioned studies. However, for up to 11-12 years after our inoculations, no seeds were produced, even though shoot production was common.

The lack of seed production may have resulted from the limited number of dwarf mistletoe infections in the stand as these experimental inoculations were the only infections present and thus pollen may have been scarce. Contrarily, the ever present damage to plants through breakage, insect feeding, or other unknown causes could account for the lack of seed production. Environmental conditions, such as reduced light in the lower crowns of trees in this dense stand or its nearness to the northern limit of this mistletoe species (Drummond and Hawksworth 1979) might also be important. Even with the excessive damage that occurred to shoots and the possibility of adverse environmental conditions, the pollen hypothesis deserves particular attention as no information is available on pollen dispersal in *A. tsugense.*

Pollen of other species of *Arceuthobium* is dispersed by wind and/or insects for distances up to 500 m, but most pollen is deposited within 10 m of the source plant (Hawksworth and Wiens 1972, Penfield *et al.* 1976, Player 1979, Gilbert and Punter 1984, Coppola 1989). The effective distance of pollen dispersal—that is, the proportion of flowers pollinated in relation to distance from the pollen source—has not been determined for any species of *Arceuthobium.* Several hundred meters separated our study stand from any natural source of *A. tsugense* pollen.

Neither the Oregon nor Canadian studies apparently followed infections for a long enough period of time to record data on infection mortality. Inoculation studies in California, however, with fir dwarf mistletoe (*A. abietinum* Engelm. ex Munz) on white fir (*Abies concolor* (Gord. & Glendl.) Lindl.) and red fir (*A. magnifica* A. Murr.) resulted in considerable mortality of infections 23-28 years after inoculation (Parmeter and Scharpf 1989). This infection mortality was also associated with branch death, but Parmeter and Scharpf (1989) attributed their demise to attack by Cytospora canker (*Cytospora abietis* Sacc.) or girdling by rodents rather than lower crown shading. Gnawing by rodents has been observed on naturally established infections of hemlock dwarf mistletoe in southeast Alaska (Shaw and Hennon 1991), but not Cytospora canker.

The lack of seed production from well established infections and the death of numerous infections through natural pruning of lower crown branches could explain the limited number of dwarf mistletoe infections that develop naturally in young stands in southeast Alaska (Shaw 1982, Shaw and Hennon 1991). Before acceptance of this conclusion, however, the development of infections from naturally disseminated seed of

A. tsugense needs to be monitored for several years to validate these experimental results. Furthermore, the levels of pollen produced, mechanisms of pollen dispersal, attributes of fruit development, and consistency of seed production on natural infections need to be determined.

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Meadow Knapweed Invasion in the Pacific Northwest, U.S.A., and British Columbia, Canada

Abstract

Most of the noxious weeds in western North America are non-native plants that have been introduced from Eurasia. Several *Centaurea* species (*C. maculosa* Lam., *C. diffusa* Lam., and *C. solstitialis* L.) apparently have become more abundant in North America than they are in their native habitats. Because all species do not have equal potential for expansion, this study was undertaken to determine the amount and distribution of another *Centaurea,* meadow knapweed, the hybrid swarm of intermediates between black knapweed (*Centaurea nigra* L.) and brown knapweed (*C. jacea* L.).

The survey began with locations on herbarium labels and was completed with locations and amounts obtained through field searches in British Columbia, Idaho, Montana, Oregon and Washington by professionals in weed education and control. Brown and black knapweed, both native to Europe and introduced in the Pacific Northwest around the turn of the century, have decreased since the 1950s. The distribution of meadow knapweed has increased, indicating that the hybrid is better adapted to conditions in the Pacific Northwest than either of its parents. Meadow knapweed was found in 4 locations in British Columbia, 2 counties in Idaho, 3 counties in Montana, 18 counties in Oregon, and 19 counties in Washington, for a total of almost 2,000 ha. New records for meadow knapweed include 3 locations in British Columbia, 2 counties in Idaho, 2 counties in Montana, 9 counties in Oregon and 10 counties in Washington. The plant is well adapted to moist meadows, irrigated pastures, riparian zones, and moist forest openings; therefore continued expansion of meadow knapweed in the Pacific Northwest is likely.

The significance of our research is in reporting new records, the success of the hybrid relative to the parent species and the type of sites susceptible to continued expansion of meadow knapweed. It also provides a baseline for monitoring continued expansion, or conversely, the success of weed control programs.

Introduction

Due to losses in rangeland forage production caused by spotted and diffuse knapweed (*Centaurea maculosa* Lam. and *C. diffusa* Lam.) and yellow starthistle (*C. solstitialis* L.) (Harris and Cranston 1979, Lacey *et al.* 1986, Roché and Roché 1988), other *Centaurea* species have been added to noxious weed lists in the Pacific Northwest. This action was taken on the rationale that controlling exotic weeds before they become widespread is less costly, both economically and ecologically. One of these species is meadow knapweed (*C. jacea* L. × *C. nigra* L.). Although it was introduced in the Pacific Northwest in the early 1900s, its potential weediness had not been investigated. The objectives of this study were to determine the amount, distribution, and types of sites it currently occupies. This information is necessary to assess the status of meadow knapweed as a noxious weed.

Meadow Knapweed Taxonomy

Meadow knapweed, also known as Protean knapweed, is a fully fertile hybrid of brown knapweed (*Centaurea jacea* L.) and black knapweed (*C. nigra* L.) (Elkington and Middlefell 1972, Marsden-Jones and Turrill 1954). Artificial hybrids can be made easily with either species as the female parent since both parents and hybrid are tetraploid, 2n=44 (Marsden-Jones and Turrill 1954, Ockendon 1975, Roy 1937). Black knapweed is native in the British Isles with hybrids being common in the southern part of England where brown knapweed has been introduced from the European Continent (Marsden-Jones and Turrill 1954). The reverse situation has been described in France where brown knapweed is native and black knapweed occurs as an introduction (Ockendon 1975). In either situation, pure forms of the introduced species do not persist for long. Populations in western North America may be the result of local hybridization or perhaps introduced from Europe as a part of a hybrid swarm (Marsden-Jones and Turrill 1954). Continued exchange of genetic material is ensured by self-incompatibility and dependence on insect pollination for sexual reproduction (Lack 1976, Marsden-Jones and Turrill 1954).

Since meadow knapweed is a confirmed hybrid, the appropriate name is *C. jacea* × *C. nigra.* The most widely used name in North America, *C. pratensis* Thuill. (Abrams and Ferris 1960, Hitchcock and Cronquist 1974, Dennis 1980, and Hawkes *et al.* 1985), is not a legitimate name

(Marsden-Jones and Turrill 1954). In Europe, hybrids or segregants of *C. jacea* × *C. nigra* have been variously named *C. debeauxii* Gren. & Godron subsp. *thuillieri* Dostal (Dostal 1976) and *C. jugens* (Gugl.) C. E. Britton, *C. pratensis* Thuill., *C. drucei* C. E. Britton, *C. surrejana* C. E. Britton, and *C. microptilon* Gren. (Clapham *et al.* 1962).

Methods and Materials

The locations of meadow, brown and black knapweed collections stored in herbaria in British Columbia, Idaho, Montana, Oregon and Washington were plotted on maps. A survey, similar to a survey of four other *Centaurea* species in eastern Washington (Roché and Roché 1988), was conducted. In 1987 a letter was sent to County Extension Agents and Weed Coordinators in Washington, the Provincial Weed Specialist in British Columbia, the State Weed Coordinator in Montana, the Program Supervisor for Noxious Weed Control in the Oregon Department of Agriculture, State Extension Weed Specialists in Washington, Oregon, and Idaho, and Herbarium curators at the Land Grant Universities in Idaho, Oregon, and Washington. The letter explained the survey, contained records of previous collections, color photographs and line drawings of the weed, and survey forms.

The color photographs showed details of the phyllary bracts of meadow knapweed, a plant in bud, and the appearance of a patch of plants in flower. Line drawings accompanied a description of meadow knapweed and the two parent species. The three plant species are differentiated by the shape of the middle rows of phyllary bracts (Figure 1).

The survey cooperators estimated the size of each population and recorded a brief description of the sites (e.g., roadside, pasture, urban) and the locations, either as legal descriptions or maps. The minimum population size was a single plant. Area occupied by the weed was estimated by length and width of infestations. Some infestations were undoubtedly missed as evidenced by historical collection sites that were not relocated. Due to inadequate label information, we could not determine whether those knapweed populations failed to survive or were not found. Some populations have received weed control treatments since being reported and were included even though the population is no longer present as reported.

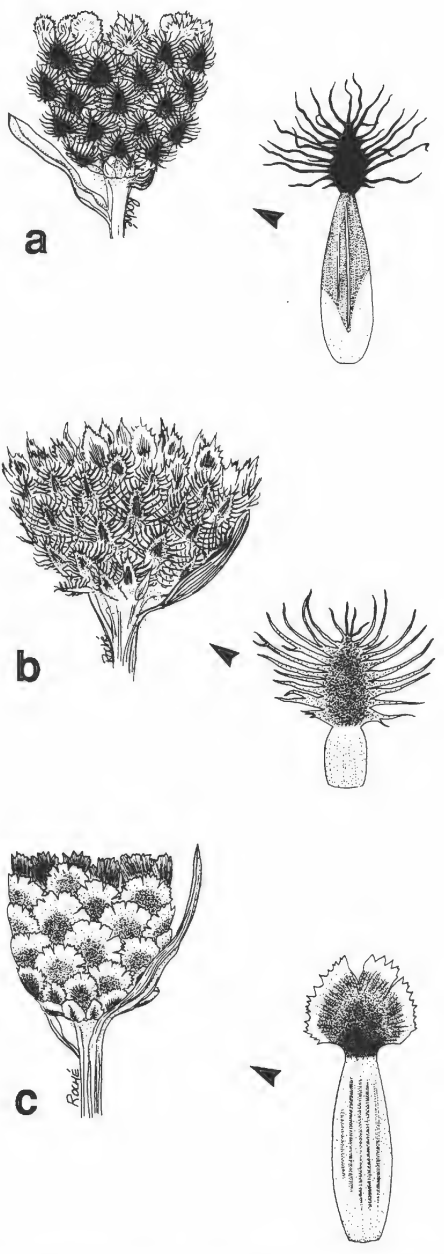

Figure 1. Involucre and detail of middle phyllary bract of a) black, b) meadow and c) brown knapweed.

The survey period included three field seasons with results compiled in February 1990. Survey

cooperators were visited in person or by phone at least once during the three year period. Collections from many of the sites in Oregon and Washington and all of the sites in Montana and Idaho have been filed in the Marion Ownbey Herbarium at Washington State University.

Results

Brown knapweed

The earliest report of brown knapweed in the Pacific Northwest is from meadows at Cedar Hill, Victoria, Vancouver Island, in 1887 (Macoun 1890). Herbarium collections of brown knapweed are dated from 1919 through 1948 (Roché and Talbott 1986). These include 3 counties in Oregon (Marion, Douglas, and Wasco) and collections in Pullman in 1923, 1924, 1938 and 1948 (Figure 2). Muenscher (1930) reported brown knapweed as a "new weed in Whatcom County, Washington, since 1920." In addition to herbarium specimens, brown knapweed was sent to Washington State University for identification from the following Washington locations: Wahkiakum County in 1949, Fargher Lake Community, Clark County, in 1959,

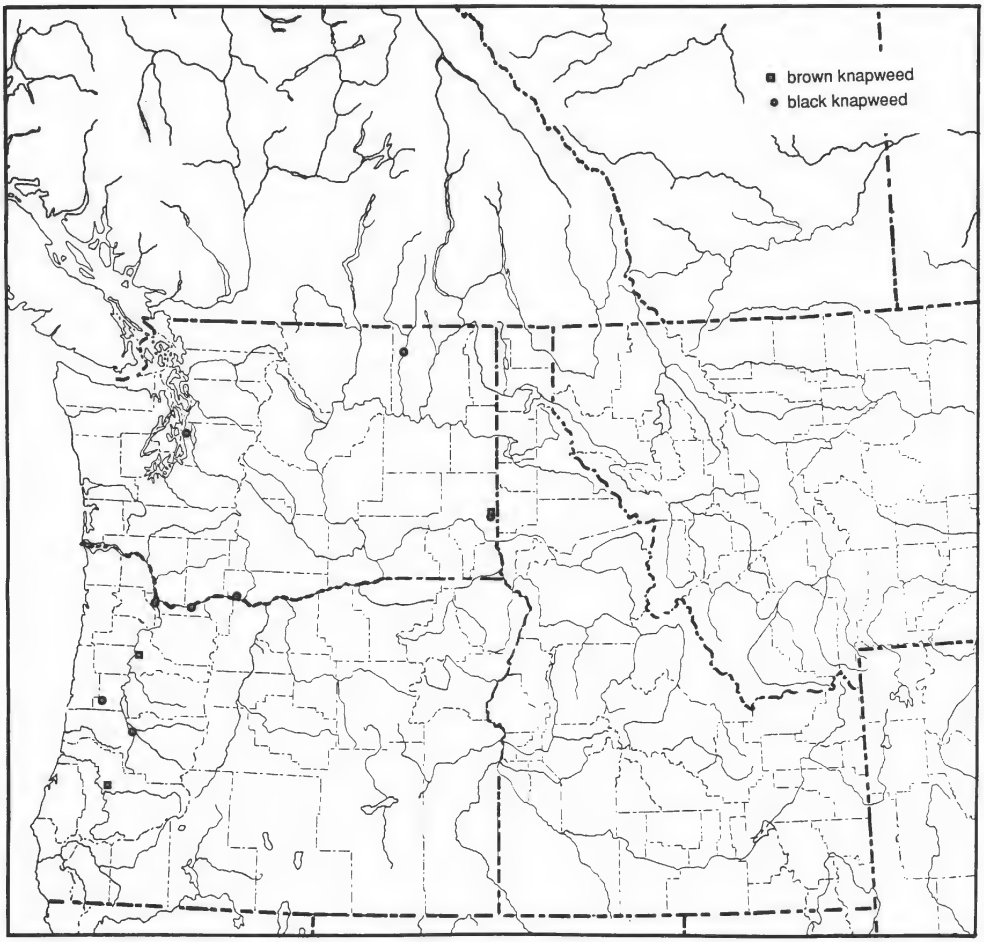

Figure 2. Collection locations of black and brown knapweed in British Columbia, Idaho, Montana, Oregon and Washington prior to 1980, according to herbarium records.

Klickitat County in 1951 and Clallam County in 1975 (Roché and Talbott 1986).

The current survey found that brown knapweed populations have persisted in Montana (Glacier National Park, Bozeman and Belgrade), in Washington (Bellingham, Ellensburg, Pullman, and San Juan Island), and in Oregon (Hood River) (Figure 3).

Black Knapweed

Black knapweed was found in Pullman, Washington, in 1895 (Nelson 1917). Herbarium collections dated from 1895 through 1955 (Roché and Talbott 1986), after which no further collections were found. It was collected from seven locations, including 4 counties in Washington and 2 counties in Oregon (Figure 2). The only collections made east of the Cascade Mountains were from Republic, Pullman, and Bingen. All of the collections from the Alsea Valley, Benton County, Oregon, were made in the 1950s. Black knapweed was sent to Washington State University for identification from Conboy Lake Basin, Klickitat County, Washington, in 1981.

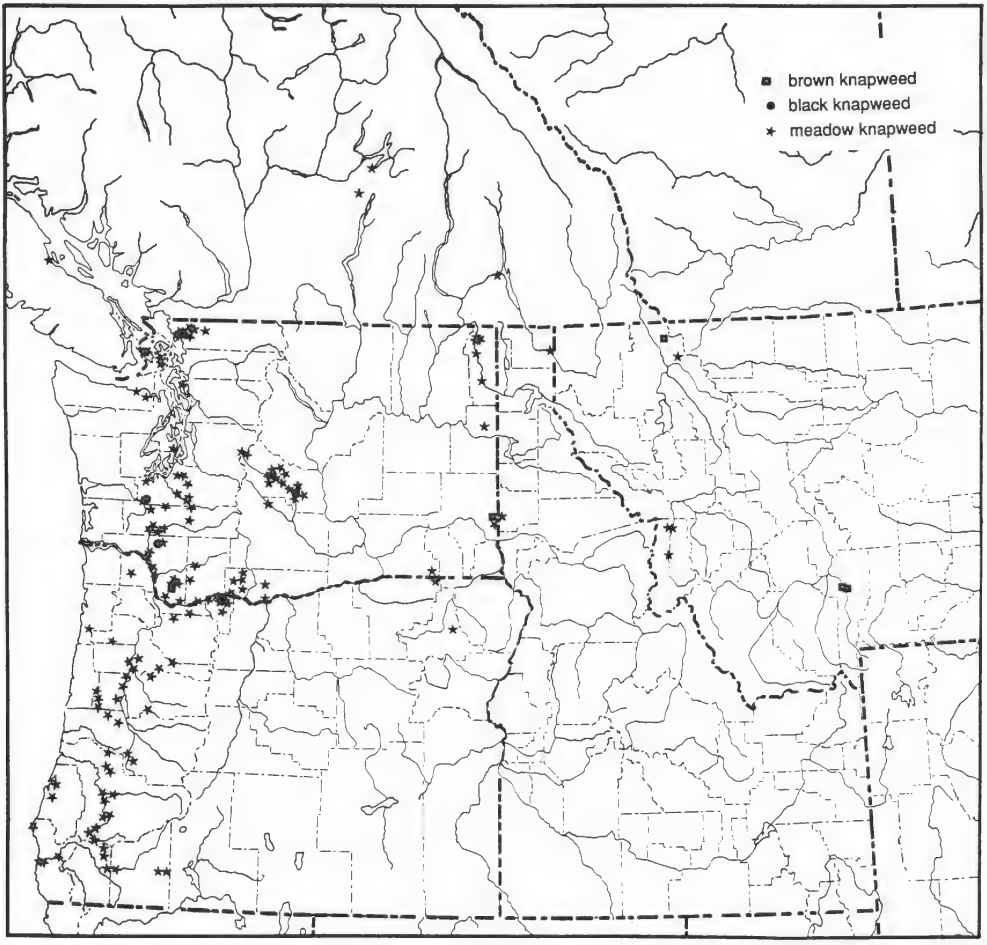

Figure 3. Distribution of meadow, black and brown knapweed in British Columbia, Idaho, Montana, Oregon and Washington, locations reported in survey as of February 1990, not including unrelocated collection sites.

In the current survey, populations containing recognizable black knapweed plants were found in Cowlitz, Thurston and Whatcom counties, Washington (Figure 3).

Meadow Knapweed

The earliest collection of meadow knapweed was in 1918 from waste areas in Eugene, Lane County, Oregon (Roché and Talbott 1986). Howell (1959) reported this hybrid to be "occasional or sometimes common along roads and in fields, variable and widespread." Before 1960 most of the meadow knapweed was collected west of the Cascade Mountains from southern Oregon into British Columbia (Figure 4). Counties in Washington included Clark, Cowlitz, King, Klickitat, Pierce, San Juan, Snohomish, Thurston, Wahkiakum, and Whatcom. Oregon counties included Benton, Clackamas, Columbia, Douglas, Hood River, Josephine, Lane, Lincoln, Marion, Multnomah, and Wasco. Meadow knapweed was also found in Lincoln County, Montana, and at New Westminster, Vancouver, Nakusp, Sidney, Westwold, and Edgewood, British Columbia.

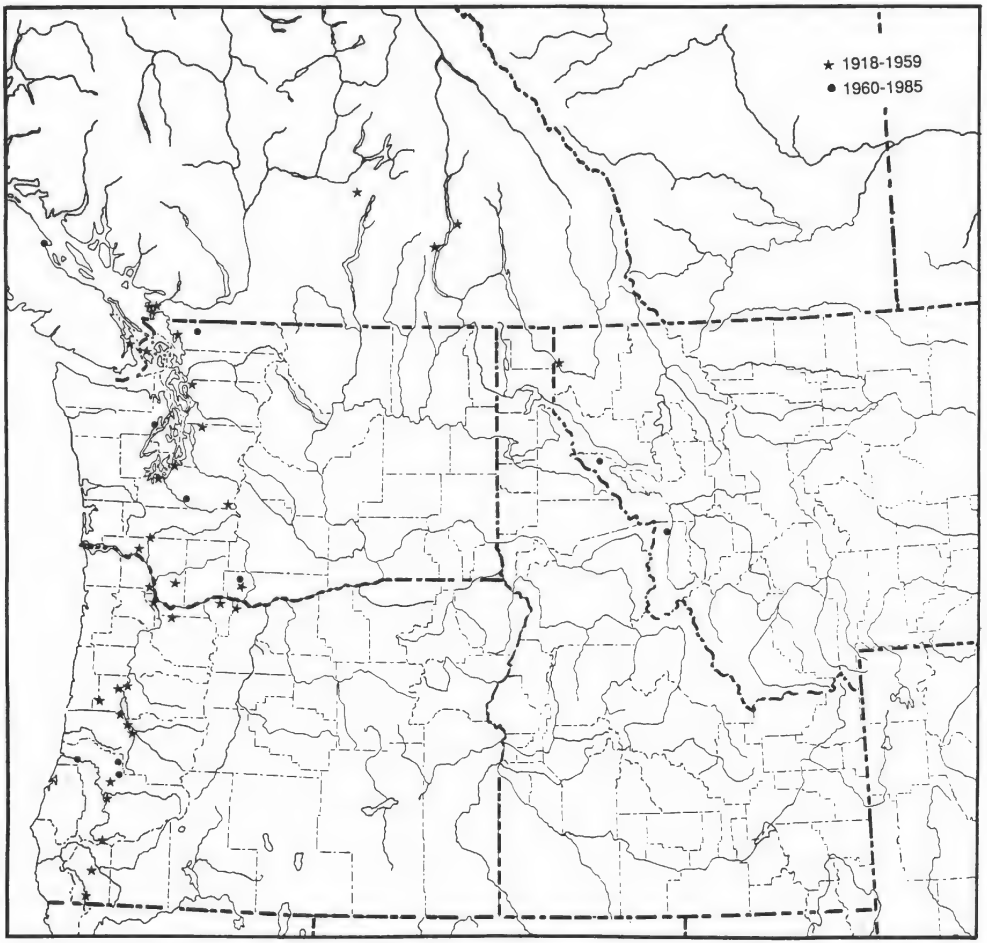

Figure 4. Collection locations of meadow knapweed in British Columbia, Idaho, Montana, Oregon and Washington, according to herbarium records.

TABLE 1. Estimated meadow knapweed population size by State or Province in hectares.

Location	Amount	Location	Amount
British Columbia		Washington Counties	
Harrop	trace[1]	Clallam	trace
Salmon Arm	trace	Clark	560
Fanny Bay	trace	Cowlitz	13
Westwold	12	Island	4
subtotal	12	King	1
Idaho Counties		Kitsap	3
Boundary	2	Kittitas	82
Latah	trace	Klickitat	51
subtotal	2	Lewis	22
Montana Counties		Pend Oreille	3
Flathead	trace	Pierce	65
Mineral	trace	San Juan	1
Ravalli	2	Skamania	1
subtotal	2	Spokane	trace
Oregon Counties		Thurston	8
Benton	5	Walla Walla	trace
Clackamas	50	Whatcom	486
Coos	0.5	Whitman	trace
Curry	2	Yakima	1
Douglas	325	subtotal	1,301
Hood River	152	TOTAL	1,877
Jackson	2		
Josephine	2		
Lane	12		
Lincoln	trace		
Linn	4		
Marion	2		
Multnomah	1		
Polk	trace		
Tillamook	trace		
Umatilla	trace		
Union	2		
Yamhill	trace		
subtotal	560		

[1]Trace is less than 0.5 ha.

In the current survey, meadow knapweed was reported from 4 locations in British Columbia, 2 counties in Idaho, 3 counties in Montana, 18 counties in Oregon and 19 counties in Washington, for a total of 1,877 infested ha (Table 1). It increased from the original distribution in the Puget Trough and Willamette Valley to both slopes of the Cascades and outlier populations in Idaho and Montana (Figures 3 and 4).

British Columbia. Early collections from Vancouver between 1937 and 1945, Nakusp in 1940 and 1946 (Roché and Talbott 1986), Sidney in 1943 and Edgewood in 1953 were not relocated. The infestation at Westwold, first reported in 1951, was estimated at 12 ha in 1988 (Table 1). Additional infestations were found at Harrop, Salmon Arm and Fanny Bay (Figure 3).

Idaho. The first records of meadow knapweed in Idaho were discovered during the survey. In 1988 a single plant was found on the University of Idaho campus in Moscow, Latah County. In Boundary County, plants were found growing along roadsides, in a lawn and in a cutover forest area in 1989 (Figure 3).

Montana. Collected near Troy, Lincoln County, in 1932 (Roché and Talbott 1986), meadow knapweed was found in Ravalli and Mineral counties by the late 1970s, along recreation trails and associated with logging activities. The meadow knapweed in Lincoln County was not relocated. Additional meadow knapweed sites were reported in Flathead and Ravalli counties in irrigated hayfields and pastures, along roadsides, trails, and an

irrigation canal, for a total of approximately 2 ha (Table 1, Figure 3).

Oregon. Meadow knapweed was not reported in the survey for Columbia or Wasco counties, where it had been collected in 1932 and 1955, respectively (Figure 4). New records included Coos, Curry, Jackson, Linn, Polk, Tillamook, Umatilla, Union and Yamhill counties (Figure 3). Meadow knapweed was most abundant in Douglas and Hood River counties (Table 1), where it now dominates pastures, fence rows, river floodplains, waste areas, and roadsides. In counties reporting less than one hectare, meadow knapweed grew only on roadsides. These sites were not restricted to high traffic areas such as Interstate 5 and cities in the main north-south corridor. Isolated plants or patches were found in relatively remote logging communities or roads (Glenn Miller, Oregon Dept. of Agric., pers. comm.). The bulk of the meadow knapweed remained concentrated in western Oregon, with the major area of expansion on the east slope of the Cascade Mountains in Hood River County.

Washington. Meadow knapweed was not found in Jefferson, Snohomish, or Wahkiakum counties, where it had previously been collected. New records occurred in Island, Kitsap, Kittitas, Lewis, Pend Oreille, Skamania, Spokane, Walla Walla, Whitman and Yakima counties (Figure 3). From the previous western Washington distribution, meadow knapweed had expanded into the mesic areas on the east slope of the Cascade Mountains around Liberty in Kittitas County and the Conboy Basin in Klickitat County. Four counties reported 91 percent of the Washington infestation: Clark, Whatcom, Kittitas, and Klickitat (Table 1). Infestations occurred on sites similar to those in Oregon; roadsides, waste areas, moist meadows, irrigated pastures, openings in forested areas and on floodplains of rivers and streams.

Discussion

Weed Introduction

These knapweeds have no obvious special mechanism for seed dispersal; seeds shaken out of the mature capitula by wind or passing animals usually fall within a few decimeters of the parent plant so that long distance dispersal is mainly by humans (Marsden-Jones and Turrill 1954). The original introductions in North America appear to have been by seeds in ships' ballast unloaded at Western seaports and intentional planting as ornamental flowers or as a forage species for livestock or bees. In the early 1900s ballast grounds at Albina and Linnton (near Portland), Oregon, were popular collecting areas for botanists who sometimes transplanted immature plants to their home gardens in order to identify the specimens later (Nelson 1917). This is likely the source of the black knapweed Suksdorf grew in his garden in Bingen in 1928 (Roché and Talbott 1986).

As an ornamental, black knapweed (also known by the common name of hardheads) was described in The Standard Cyclopedia of Horticulture (Bailey 1922) as "a very striking border plant, useful in dry or open places." Brown and black knapweed are still available in retail seed catalogs, listed by name, and in "wildflower" mixes. The two parent species appear to have been planted on college campuses or perhaps became established through careless handling of collected materials: brown knapweed at Willamette University, Salem, 1919, and Pullman, 1923; black knapweed in Pullman, 1895, and on the campus of the University of Washington, Seattle, 1935 (Roché and Talbott 1986). Some counties reported movement of meadow knapweed by individuals transplanting it as a wildflower (Blair Wolfley, Clark County, and Mary Fries, Lewis County, pers. comm.).

Brown knapweed was planted for hay and forage in eastern Canada in the 1850s (Rousseau 1968). A farmer near Freilighsburg, Missiquoi County, planted it as a source of pollen for honey bees around 1880 (Moore 1969). Meadow knapweed was cultivated as a source of winter forage near Roseburg, Douglas County, Oregon in 1952 (Howell 1959).

Although herbarium collections are an incomplete record of the historical distribution, they indicate that meadow knapweed was probably introduced as a hybrid and did not arise exclusively from brown and black knapweed hybridization in the Pacific Northwest. Pullman is the only location where both parents were collected: black knapweed in 1895 and brown knapweed from 1923 to 1985 and no hybrids have been found there. The closest meadow knapweed was an isolated patch found in 1986 approximately 30 km south of Pullman, near Uniontown. Both brown and black knapweed were collected earlier than the hybrid, and the frequency of collection has declined with time. The parent species were apparently introduced independently and met one of three fates: they were absorbed

into hybrid populations, persisted as relatively "pure" populations, or failed to survive. In contrast, meadow knapweed collections increased. The survey verified the trend of increasing distribution of the hybrid while the parent species declined. As judged by its increase in distribution, meadow knapweed is better adapted to conditions in the Pacific Northwest than either of its parents. The variability in its genetic makeup has undoubtedly been an asset in exploiting a variety of habitats, providing the basis for natural selection (Turrill 1964). Hybrid vigor may also be important. Marsden-Jones and Turrill (1954) found no morphological differences between seedlings of brown and black knapweed, but hybrid seedlings grew faster.

Weed Migration

The two most important forces in the continued migration of meadow knapweed appear to be water and vehicles. Meadow knapweed was found growing on the floodplains of the Columbia, Umpqua, Rogue, Naches, Teanaway, Willamette, and Yakima rivers, Swauk and Spring creeks, and along irrigation ditches. Meadow knapweed infestations from vehicle-borne seeds range from the median of Interstate 5 to remote forest roads. Populations found along roadsides, in campgrounds, urban and industrial sites, including old mill yards, all implicate vehicles. Lacking a pappus, seeds may be carried in mud on equipment or vehicles.

Controlling scattered infestations while they are small outliers is important in containing the spread of an alien species (Moody and Mack 1988). The widely scattered infestations of diffuse and spotted knapweed in the 1950s (Roché and Talbott 1986) increased to major infestations of 173,000 ha of diffuse knapweed in Washington (Roché and Roché 1988) and 1,911,000 ha of spotted knapweed in Montana (Lacey 1989). While the ecologic amplitude of meadow knapweed appears to be narrower than that of diffuse or spotted knapweed, the potential invasion sites are more productive or environmentally sensitive (e.g., riparian areas). Meadow and riparian sites can produce 3 to 10 times more biomass than semi-arid sites (Roath 1985, Quigley *et al.* 1989). Athough previously cultivated for winter forage, meadow knapweed's coarseness makes it generally less palatable to livestock than associated species. Pastures near Hood River, Oregon, have been left idle following invasion and dominance by meadow knapweed (Rob Varga, Hood River County Weed Control, pers. comm.). However, palatability is relative and we observed prostrate plants in closely cropped pastures in Klickitat and San Juan counties.

In addition to detrimental effects on forage production, meadow knapweed is an undesirable invader of native plant communities, especially on floodplains and in disturbed forests. When exotic species invade natural communities they reduce natural diversity by causing extinctions and shifts in patterns of relative abundance (Temple 1990). Although it is probably too late to eradicate meadow knapweed in western North America, large infestations can be contained. Recent expansion of meadow knapweed distribution justifies local eradication of the small infestations.

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1

STRIKE-INDUCED CHEMOSENSORY SEARCHING (SICS) IN RATTLESNAKES: RECENT STUDIES ON TRAIL FOLLOWING, REPEATED TESTING, AND CHEMICAL LEARNING. David Chiszar and Hobart M. Smith, University of Colorado, Boulder.

Prairie rattlesnakes (Crotalus viridis) typically release adult rodent prey immediately after striking them, allowing the rodent to wander from the site of attack while venom takes effect. Within 5 min of the strike, snakes begin to flick their tongues at a high rate as they search for the rodent's chemical trail. Recent experiments have studied the stability of SICS over repeated tests. Also, we have demonstrated that rattlesnakes acquire information about the prey's chemical identity during the strike. This information is retained for 2 hr and is used to guide post-strike trail following. Finally, new data will be presented on the question of how strikes trigger SICS.

2

FACTORS INFLUENCING VENOM EXPENDITURE BY RATTLESNAKES. W. K. Hayes, Southern College, Collegedale, Tennessee.

Six laboratory studies were conducted to determine how and why rattlesnakes allocate venom supplies. Strike behavior was analyzed via slow motion videotape review. Enzyme-linked immunosorbent assay of whole-animal homogenates was used to quantify mass of venom expended by snakes. Results may be summarized as follows. (1) Adults release about a quarter to a third (14 mg) of available venom when biting mice, and about 89% of released venom is successfully injected into prey tissues. (2) Venom expenditure during feeding increases exponentially with length of snake. (3) Hungry snakes expend less venom than well-fed snakes. (4) Rattlesnakes strike and release mice, but hold on to and likely expend more venom when feeding on sparrows. (5) With experience, juvenile snakes attempt to inject more venom into larger mice. (6) Duration of fang contact is less during defensive strikes at rats (0.07 sec) than predatory strikes at mice (0.15 sec). These findings suggest that rattlesnakes control venom expenditure and utilize several strategies which maximize envenomation and feeding success in different circumstances. Research supported by NSF grant BNS-8813271.

3

PRELIMINARY SYSTEMATIC STUDIES ON RHIZOPLACA (LICHENIZED ASCOMYCOTINA). Bruce D. Ryan, Arizona State University, Tempe, AZ, and Roger Rosentreter, Bureau of Land Management, Boise, ID.

At least two new vagrant taxa of Rhizoplaca, plus R. baranowii and fertile material of R. haydenii, are now known in North America. The R. melanophthalma complex includes an extreme range of both attached and vagrant morphotypes. The "placodiolic acid strain of R. melanophthalma" is a distinct taxon, more similar to R. subdiscrepans (in the R. chrysoleuca complex). In eastern North America, the squamulose morphotypes of R. chrysoleuca s. lato always contains pseudoplacodiolic acid and occur without the umbilicate forms, but in Eurasia and western North America, the squamulose morphotypes usually contain placodiolic acid and are mixed with several umbilicate forms with various cortical chemistries, colors and morphologies. The Californian endemic taxa, R. marginalis and R. glaucophana, and several South American umbilicate lecanoraceous taxa (including ones with short spermatia, and one with xanthones instead of usnic acids), may be distinct from Rhizoplaca s. stricto.

4

SLUMPS AND FLOODS, LEWISTON BASIN, IDAHO AND WASHINGTON. William N. Laval, Lewis-Clark State College, Lewiston, Idaho.

Slumps in an area of more than one square mile in the southwestern part of Lewiston exhibit the classical down at the heels displacement as well as scalloped indentations into the east side of the Snake River valley. In contrast a few miles to the south slumping of similarly low-dipping strata likewise associated with the Sweetwater Creek interbed between the Wanapum Basalt and the Saddle Mountains Basalt exhibits less coherency. It is postulated that Spokane-Missoula floods furnished the requisite pore-water pressure for the classical Lewiston slumps, whereas those to the south in the state of Washington developed above the shorelines of flood-produced lakes, as well as the crest of the Bonneville flood. Slumping occasioned by the rise of the Lower Granite Reservoir and an unusual amount of precipitation during March, 1975 suggested the possibilities for glacial stage processes. A large golf course on the moraine-like Lewiston slump block terrain, and housing developments on it and the brink of the slump escarpment add human interest.

5

REVEGETATION OF FIRE-ALTERED HABITAT IN THE SNAKE RIVER PLAIN. M.Pellant. Bureau of Land Management, Boise, ID. Frequent wildfires have dramatically reduced shrub cover and native plant distribution. Attempts to restore perennial vegetation is hampered by frequent droughts, poor germination periods and competition from alien, annual species. Early revegetation efforts utilized introduced, perennial wheatgrasses because of their superior seedling vigor and drought tolerance. Seeding of shrub species in revegetation projects is undertaken if wildlife habitat values are high. Shrub seeds are often hard to distribute with conventional seeding equipment. Techniques have been developed to successfully establish big sagebrush *(Artemisia tridentata)*, winterfat *(Ceratoides lanata)* and forage kochia *(Kochia prostrata)*. Protection of unburned shrublands is accomplished by establishing fire resistant vegetation i.e. greenstrips at strategic locations on fire prone rangelands. Research is in progress to develop native shrub cultivars that are palatable and capable of resprouting after a fire.

6

FIRE ECOLOGY OF THE SNAKE RIVER PLAIN. S.C. Bunting. Univ. of Idaho, Moscow.

Fire has been an important factor in the development of the vegetation of the Snake River Plain. Prior to Euro-American settlement, fire helped determine the physiognomy and species composition of many communities. The occurrence of fire varied widely throughout the region depending upon the vegetation present. This impact can be detected in many historical documents and inferred from species response to fire. During the post-settlement period, the occurrence of fire has increased throughout much of the Snake River Plain. The introduction of annual grasses, particularly Bromus tectorum, has altered fuel loads and fuel distribution which in turn has changed fire intensity and extent. Increased human activity has resulted in greater numbers of ignition sources. The decreased fire-free-interval has greatly modified the pre-settlement role of fire and the distribution of many species.

7

VEGETATION OF LOWER SNAKE RIVER PLAINS. M.Hironaka. Univ. of Idaho, Moscow.

Vegetation of this portion of the Snake River Plains is of two basic types, Wyoming sagebrush and salt desert shrub communities. In the 7-8" precip zone, sagebrush is replaced by shadscale and/or winterfat. Soils derived on the Payette Formation, produce a mosaic of salt desert shrub communities. The combination of low rainfall, soil salinity, soil texture and chance explain the distribution pattern of these communities. Permanent loss of sagebrush and salt desert halfshrubs have changed the physiognomy over extensive areas because of introduction of cheatgrass and attendant fires.

8

THE EFFECTS OF ANIMAL DAMAGE UPON THE GROWTH OF WESTERN HEMLOCK SEEDLINGS IN RIPARIAN ZONES OF THE OREGON COAST RANGE. J. M. Hyatt E. C. Cole and M. Newton, Oregon State Univ., Corvallis.

The effects of deer and lagomorph damage on western hemlock and its subsequent growth were examined during the first 4 years after planting. The study utilized a Nelder/replacement series experiment which focused on the competitive effects among hemlock, alder and salmonberry. Herb and shrub development was suppressed on half the plots and unrestricted on the remainder. Seedling density ranged from 1284 to 85470 seedlings/ha. Cover ranged from 0% to 100% within a meter radius of each seedling. Growth of seedlings exhibiting similar levels of damage was compared when growing under different levels of competition. As vegetative competition increased, seedling growth decreased. The occurrence of deer damage decreased as cover increased, whereas lagomorph damage increased as cover increased.

9

ASPECTS OF VECTOR AND RASTER-BASED GIS ANALYSES FOR PARK HABITAT MANAGEMENT
Philip D. Tanimoto, NPS Cooperative Park Studies Unit, Dept. of Wildlife Resources, Univ. of Idaho, Moscow

An ecological habitat map of Lake Chelan National Recreation Area was developed and formatted as vector and raster-based GIS coverages. Vector processes were used to analyze effects of past human impacts on snag densities. In accessible areas snag densities averaged less than 0.5/ha while in more remote forests densities approached 2.0/ha. Raster functions were more adept at "moving window" habitat diversity analyses than were vector. Land use data were combined with habitat and diversity maps to identify areas under potential threat of development. Results provided objective suggestions for prioritizing ground-based investigations into habitat protection.

10

NATURAL REGENERATION IN SOUTHWESTERN OREGON FORESTS. R. Lewis and E. Park, Bureau of Land Management, Medford, Or.

Reforestation strategies for the Douglas-fir region have relied on planting in clearcuts with control of competing vegetation. Natural regeneration has been regarded as too uncertain and the time required to achieve success too long. Observations following the wild fires of 1987 indicated that conifer regeneration could be prompt under favorable conditions and that the presence of pioneering hardwoods did not interfere with conifer regeneration. Douglas-fir regeneration increased for the three years following fire on cool, mesic sites with residual overstories, despite the absence of good seed years. Natural pine regeneration occurred on harsher sites. Similar results were noted in a study installed in a timber sale on a harsh site in 1985. Stocking trend varied with the degree of site disturbance. These observations indicate that natural regeneration can be adequate in the sub-region with site disturbance and retained canopies and that such regeneration can occur promptly.

11

LICHEN COMMUNITIES OF OLD GROWTH WESTERN HEMLOCK FORESTS AND SHOREPINE MUSKEGS OF THE TONGASS NATIONAL FOREST, SE ALASKA. L.H. Geiser, U.S.F.S., Petersburg, AK.

Lichen diversity and abundance were estimated at 20, 42' radius shorepine plots by measuring the % cover of each species on the first 30 cm. of all branches up to eye-level on ten trees. At 22 hemlock plots, the stick with the most lichens was collected every 3' along 8 evenly spaced radii. The best 30 cm. sections of 120 sticks were measured for lichen diversity and abundance. Various other physical and vegetative parameters were recorded at each plot.

The number of species at hemlock plots ranged from 11 to 33, averaging 16.6 (±3.2). At pine plots, the number of species/plot ranged from 8 to 31, averaging 20.5 (±6.2). Species abundant in both habitats were: Alectoria sarmentosa, Sphaerophorus globosus, Platismatia glauca, P. norvegica, Bryoria trichodes, B. glabra, Cladonia bellidiflora, C. squamosa, C. umbricola, Hypogymnia duplicata, H. enteromorpha, and H. vittata. Species common only at muskeg sites were H. inactiva, H. oceanica, Cladinas, Siphula ceratites, C. maxima, C. uncialis, C. crispata, C. furcata, C. cornuta, C. umbricola, B. carlotte, B. lanestris, B. oregana, B. cervinula, and B. bicolor. Species common only at hemlock sites were Lobaria oregana, L. linita, Peltigeras, Nephromas, Usneas, P. lacunosa, and C. ochrochlora.

12

ECOLOGY AND DISTRIBUTION OF GRAND FIR WEST OF THE CASCADES. Robert Van Pelt, University of Washington, Seattle.

The role of grand fir (*Abies grandis* (Dougl.) Lindl.) in the coastal region of the Northwest is poorly understood. A minor component of coastal forests, grand fir is found in a scant collection of low elevation habitats. Because of this infrequency, grand fir plays a very minor role in forestry in west-side forests. East of the Cascade Crest it is a major forest component and has been researched from many differing viewpoints including ecology, silviculture, fire ecology, and pest and disease management. Much of this research is of little use when applied to populations occurring on the west-side, due in part to the great differences in the forests between the two areas. Autecological characteristics of grand fir help explain its relative disadvantage throughout most of the coastal region. The presence western hemlock and western redcedar produce a light environment in which grand fir cannot regenerate. Frequent fires and large areas without western hemlock and western redcedar allow for successful regeneration east of the Crest. Although optimal situations for growth and development occur in western Washington and coastal British Columbia, they make up less than one percent of the forest area. An examination of the scant and sporadic distribution in the coastal region gives important clues as to its ecological role in west-side forests. This work identifies four distinct habitats in this region, each with a differing disturbance pattern, allowing it to persist in isolated locales in the densely forested west-side region.

13

WHAT IS A 'VENOMOUS' SNAKE? K. V. Kardong, Washington State Univ., Pullman.

A distinction should be made between a "toxin" and a "venom" as applied to animal secretions. Failure to draw a distinction has led to unfortunately narrow biological and medical views of many animal poisons. Venoms are released by true venom glands in advanced snakes such as viperids and elapids, and perform the biological role of rapidly killing the prey. Although homologous to the venom gland, the Duvernoy's gland in most colubrids releases a secretion that is usually not used to rapidly kill prey or conspicuously in defense. Thus, despite finds that in some species such secretions are toxic, it does not follow that this toxic secretion makes the snake venomous. Such a distinction should encourage biologists to adopt an independent course in pursuing questions of snake venoms and encourage the search for other biological roles and other chemical properties of Duvernoy's secretion that are of significance to the snake rather than to the pharmacologist.

14

OREGON'S LICHENS AND BRYOPHYTES: ASSESSING RARITY. John A. Christy, Oregon Natural Heritage Data Base, Portland.

The Oregon Natural Heritage Data Base has tracked the occurrence of rare lichens, liverworts and mosses since 1983. Over the last six years, sixteen species have been nominated for listing by the Data Base, but lesser-known taxa no doubt have been overlooked by this individual-based approach. Until recently, no attempt has been made to rank the relative rarity of all 1000 species in the state, in part because comprehensive checklists were not avaiable. Global ranks have been assigned nationally, but individual heritage programs must determine state ranks. Significant obstacles remain in ranking Oregon's taxa with any degree of confidence, because the distribution of many of these within the state is still poorly known.

15

SIXTEEN YEAR RESULTS OF THE IUFRO DOUGLAS-FIR PROVENANCE - PROGENY TEST. O. Sziklai, University of British Columbia, Canada.

The Douglas-fir seed collection carried out by IUFRO Section 22 on the west coast of North America in 1966 provided samples from 1,818 trees, representing 124 provenances.

Morphometric characteristics of cone and seed were measured or described, seed yield was determined, and seeds were germinated. A provenance progeny test was established in 1971. The height was measured in 1973, 1975, 1978 and 1986.

Volume was calculated after the 1986 height and diameter measurements.

The Coast and Interior varieties could be separated out with certainty using seed morphology traits.

Early height measurements after 5 years correlates well with 16 year height of the fastest and slowest growing provenances.

Individual trees within most of the provenances exhibited large variation.

16

AN INTERDISCIPLINARY APPROACH TO AIDS EDUCATION: TWO YEAR SUCCESS STORY. Russell I. Centanni, Boise State Univ., Boise.

HIV disease and its end stage AIDS is more than a biomedical problem. This disease cuts across the fabric of humanity and asks that we examine fundamental values and behaviors. Such an examination requires an interdisciplinary approach. This paper reviews the format used in three five week, one credit, workshops offered during the Fall 1989 and 1990 semesters. Team taught by professors of microbiology and social work, 198 students were introduced to issues ranging from sexuality to death and dying, homophobia to ethics, disease transmission to safer sex negotiation, health care and social services delivery to economics. A knowledge/attitude/behavior survey was completed. Results to be presented will show a dramatic increase in knowledge and an altering of attitudes towards HIV disease and AIDS. With current data suggesting a 0.5% HIV+ incidence rate on American college campuses, this presentation will provide a usable model for HIV/AIDS education.

17

SONGS AND CALLS IN A FREE-LIVING BIRD: SEASONAL PATTERNS AND THEIR RELATIONSHIP TO CIRCULATING TESTOSTERONE LEVELS. A. M. Dufty, Jr., Boise State Univ., Boise, ID.

Laboratory studies have established that production of bird song is closely-related to the steroid hormone testosterone (T). However, surprisingly little information is known about the relationship among vocalizations and T in free-living birds. I conducted a season-long census of vocal activity in free-living brown-headed cowbirds (Molothrus ater). Cowbirds have two major vocalizations, songs and flight whistle (FW) calls; these are acoustically distinct but have functional overlap. I also collected blood samples from the cowbirds which was assayed for T. All male vocalizations were produced at peak levels early in the season, when dominance rank and mate selection are determined, and all were significantly correlated with each other. However, only songs were significantly correlated with plasma levels of T; FWs were not. This suggests that songs and calls may have different physiological bases, despite their functional overlap.

19

WETLANDS INVENTORY METHODS; SCIENCE APPLIED TO PUBLIC POLICY. M.M.Folsom, Eastern Washington Univ., Cheney.

An inventory of wetland sites that is conducted by the best of scientific methods may not satisfy funding authorities, who are driven more by policy considerations than by rules of scientific inquiry. Similarly, the budget and time constraints imposed by the funding agencies may not meet the sense of rigor of the wetlands scientist. This may not be the style of science that we want to do, but it is the style of science that society is willing to pay for. The risk is not to the intellectual integrity of the individual scientist, rather that this type of minimal research, once concluded, becomes translated into the iron paragraphs of regulations and is never re-examined. Is imperfect science any better than no science at all?

18

THE ENERGETICS OF THE SIDEWINDER, CROTALUS CERASTES
Stephen M. Secor Department of Biology, UCLA, Los Angeles, CA 90024.

Rates of energy acquisition and expenditure have major influences on countless aspects of an organism's life. This study explores the energetics of the sidewinder, Crotalus cerastes, by investigating its thermal biology, foraging tactics, field metabolic rates, and net cost of transport. Sidewinders experience a wide range of body temperatures and are active with body temperatures ranging from 12 - 38 C. As a sit and wait forager, they feed upon mobile prey and have a low rate of prey capture. Field metabolic rates of free-ranging sidewinders during their activity season are significantly low (0.03 - 0.09 ml CO_2/g h). In search of new foraging sites, sidewinders will travel considerable distances (> 900m) in a night, though the net cost of transport for sidewinding is remarkably low (0.41 ml O_2/g km).

20

VOLCANOLOGY AND ECONOMIC GEOLOGY: DOOLEY MOUNTAIN, OREGON. C.C. Unsworth, Boise State University

Detailed geologic mapping and geochemical studies on a volcanic dome and associated pyroclastic rocks near Dooley Summit (approximately 20 miles south of Baker City, Oregon) are providing insights into the physical volcanology and geologic history of the area. The work is also providing a geologic data base for determining future economic mineral resource potential.

The rocks are part of the Miocene (14 Ma) Dooley Volcanics and are predominatly composed of rhyolite flows, domes and dikes. These rhyolites range in composition from 74 to 81% SiO_2, suggesting hydrothermal silica may have been introduced into many of the rocks sampled. The rhyolites intruded and flowed onto heterolithologic tuff breccias which probably formed as pyroclastic flow deposits in the early stages of the volcanic eruptions. The flow-dome complex is possibly associated with the formation of the northern portion of the Basin and Range Province.

Anomalous abundances of trace elements, such as Au, Ag, As, Sb, Pb, and Hg, have been found to be closely associated with the most prominent rhyolite dome in the area. This suggests the dome intrusion may have developed a hydrothermal system (hot springs) and the potential for epithermal precious metal mineralization.

21

LONGITUDINAL ZONATION OF TRICLADS IN ROCK CREEK (IDAHO). W.H. Clark, Idaho Department of Health and Welfare, Boise, and Smith Museum of Natural History, College of Idaho, Caldwell and A.M. Hampton Castleton State College, Castleton, Vermont.

A ten year water quality monitoring project of Rock Creek, Twin Falls County, Idaho has been completed. Best management practices have been implemented to improve water quality through control of suspended sediment and nutrient pollutants. At downstream sites water quality is poor and there is a low diversity of macroinvertebrates and more "pollution tolerant organisms." Upstream, water quality improves as does the diversity of macroinvertebrates and the number of "clean water organisms." Triclad turbellaria are distributed along the length of Rock Creek (975 to 1445 m). Dugesia dorotocephala (Woodworth, 1897) is abundant at the lower and middle sample stations. Further, it has been collected from these sites prior to extensive abatement measures. At upstream sites Dugesia is supplanted by Polycelis, presumably Polycelis (P.) coronata cornata (Girard, 1981). These findings add to the knowledge of habitat requirements and tolerances for these two triclads.

22

POPULATION STRUCTURE, GROWTH, AND SIZE OF TAILED FROG (ASCAPHUS) TADPOLES FROM A LOWLAND STREAM IN NORTHWESTERN WASHINGTON. H. Brown, Western Washington University, Bellingham, WA.

The size of tadpoles at various stages of development was determined by monthly collections (Feb.-Oct.) at Austin Ck (near the southwest end of Lake Whatcom). Females lay eggs in July, and tadpoles develop for two years and metamorphose during July/August. There are two groups of tadpoles in the autumn: hatchlings with total length = 24.7 mm and body weight = 150 mg, and one year tadpoles, 45.0 mm and 1100 mg. During April/May of the next year the younger tadpoles average 33.9 mm (range, 24.4-45.8) and 441 mg (123-1104), and the older group is 50.7 mm (46.8-56.2) and 1656 mg (1273-2289). During July/August the nonmetamorphic tadpoles average 43.3 mm and 935 mg and the metamorphic tadpoles, 42.7 mm and 1181 mg. This population has great variablity in body size during development and metamorphosis. Two rare anomalies were found: one albino and four situs inversus viscerum.

23

SOME OBSERVATIONS ON LICHEN DISTRIBUTION IN YELLOWSTONE NATIONAL PARK. S. Eversman, Montana State University, Bozeman.

Lichens have been collected from all apparent substrates and elevations in relatively accessible sites in Yellowstone Park. Species on soil and rock (130 in number) range from those best associated with warm dry grassland (Fulgensia fulgens, Lecanora novomexicana) to arctic-alpine species (Dactylina madreporiformis, Thamnolia subuliformis). Of about 40 epiphytic species, most are rather restricted to bases of conifers, above 2 m high on trunks among branches, on branches, and on sagebrush. Most species have a boreal distribution. Several species in genera such as Cetraria and Hypogymnia are abundant in locations adjacent to the park but have not yet been collected in the park. Cladina mitis is common in some geyser basins. Rhizocarpon geographicum is frequently at the mouth of steaming fumaroles.

24

TRADE-OFFS BETWEEN ALLOCATION TO REPRODUCTION AND GROWTH IN AN ALPINE ASTRAGALUS. Wayne R. Owen, University of California, Davis.

Astragalus kentrophyta var. implexus is a long-lived perennial legume which inhabits alpine regions in the Great Basin Province of the western U.S.. A field experiment was conducted in the White Mountains of California to determine: 1. If and to what extent does resource availability constrain growth and reproduction in this species, and 2. The nature of the interaction between growth and reproduction. Supplemental water and mineral nutrients (NPK) were provided to some plants while others were protected from herbivores or released from the competitive influence of neighbors. Data on growth and seed production were collected over a two year period. A trade-off between growth and reproduction was identified in all plants except those released from competition. Allocation to reproduction did not vary between treatment groups in either year however, allocation to growth appears to be labile and influenced by both current and previous conditions.

25

A MATRIC-PRIMING TECHNIQUE FOR ENHANCING THE GERMINATION CHARACTERISTICS OF SMALL-SEEDED GRASS SPECIES. S.P. Hardegree, USDA-ARS, 800 Park Boulevard, Plaza IV, Suite 105, Boise, ID 83712.

The purpose of this study was to evaluate a matric-priming technique for enhancing germination of small-seeded grass species. The matric-priming technique used here differed from osmotic-priming methods in that the seeds were separated from the priming solution by a cellulose membrane. An advantage of matric-priming is that the seeds remain surface-dry during the procedure. Surface-dry seeds do not have to be rinsed of osmotic solution prior to planting and are easily monitored for water content during the treatment. Matric-priming at high water potential and short duration was found to enhance germination of all species tested. Seed water uptake measurements indicated that the increased germination rate of primed seeds was due primarily to a decrease in the lag time of imbibition.

26

EPIPHYTIC LITTERFALL IN DOUGLAS FIR - HEMLOCK STANDS OF VARYING AGES. *B. McCune*, Oregon State Univ., Corvallis.

Epiphytic litter was sampled in Sept. 1990 with 20, 2-m radius plots in each of three Douglas-fir-western hemlock stands in the Cascade Range, ages 95, 145, and 400+ years. Epiphytes were sorted into four functional groups: cyanolichens, alectorioid lichens, other macrolichens, and bryophytes. A standard error of 10% of the mean for each functional group of lichens requires 9-27 of these plots (high end in old growth). Bryophyte litterfall was far more variable from plot to plot than lichen litterfall, with 200 or more plots needed for a similar level of sampling error. Bryophytes and cyanolichens were virtually absent from litterfall in the younger stands, but averaged 12 and 18 kg/ha respectively in the old growth. Alectorioid lichens were equally abundant in the old-growth and 145-yr stand (6 kg/ha) but had only 0.6 kg/ha in the 95-yr stand. Other macrolichens (mainly *Hypogymnia* and *Platismatia*) were most abundant in the younger stands (10-15 kg/ha), with 4 kg/ha in the old growth. The method shows promise for assessing epiphyte abundance in tall forests. Future work will calibrate epiphyte litterfall against epiphyte biomass and assess seasonal and yearly variability in litterfall.

27

OLD GROWTH RIPARIAN BIRDS OF THE OLYMPIC PENINSULA: EFFECTS OF STREAM SIZE ON COMMUNITY STRUCTURE. P.A. Lock and R.J. Naiman, University of Washington, Seattle.

Spring breeding bird communities of large and small rivers on the Olympic Peninsula were censused and compared. Six sites total were surveyed: Three rivers >100 m. wide and three rivers <20 m. wide. At each site vegetation composition and structure were characterized.

Birds were censused between 15 May 1990 and 30 June 1990. Thirty-two species were identified in the 1084 birds detected. Of these 32, 61% were common to both large and small rivers, 32% occurred only on large rivers and 6% occurred only on small rivers. The three most common species on all sites were the Western flycatcher, Golden-crowned kinglet, and Winter wren. Bird abundance, species richness, and community diversity were higher on large rivers than on small rivers.

The objectives of the study were to (1) provide a baseline description of Old growth riparian bird communities, (2) determine whether there is a difference between bird communities along large and small rivers, and (3) define what aspects of the fluvial corridor are most important in determining bird abundance and community structure.

Keywords: Olympic Peninsula, riparian, birds

28

SOIL AND PLANT RELATIONSHIPS AT A MARINE HEADLAND, STRAIT OF JUAN DE FUCA, WASHINGTON. S. K. Rust, University of Washington, Seattle.

Soil was sampled along an observed forest/grassland vegetation gradient at a marine headland, Iceberg Point, Lopez Island, Washington. Samples were taken from three replicate sites chosen to represent four plant community composition classes. Determinations of pH, electrical conductivity, total carbon, and extractable metal content were made. Observed differences in soil pH, electrical conductivity, and cation concentrations correspond to predicted deposition of marine aerosols but also reflect influences of the vegetation. Soil chemistry, and perhaps nutrient availability, may be an important environmental factor in determining plant community composition and distribution.

29

RED-TAILED HAWK PREDATION ON SNAKES: THE EFFECTS OF WEATHER AND SNAKE ACTIVITY. S. Grothe, C.R. Peterson, and C.H. Trost. Idaho State University, Pocatello, ID.

To examine the effects of weather and snake activity on red-tailed hawk (*Buteo jamaicensis*) predation on snakes, we observed the number, type, and times of prey delivered to hawk nests. The study was conducted during the birds' nesting period (late April to late June) at the Snake River Birds of Prey Area in southwestern Idaho. We watched two nests, one per day from either 0700 to 1400 or 1400 to 2100 hrs. Thermal conditions were measured with copper snake models, thermocouples, and a datalogger. We used automated telemetry systems to measure the body temperatures and activity patterns of five adult gopher snakes (*Pituophis catenifer*) outfitted with activity and temperature-sensitive radiotransmitters.

Snakes were an important prey item, making up 42% (30 of 72) of the prey items observed during the 189 hours the nests were watched. These 30 snakes made up approximately 65% of the hawks' estimated dietary biomass. Fifteen of the snakes were gopher snakes, seven were racers (*Coluber constrictor*), and eight could not be identified. All but one of the snakes were delivered between 0930 and 1800 hours. No snakes were delivered when model temperatures were lower than 15°C; 90% of the snakes were delivered when snake model temperatures exceeded 27°C. When the analysis of the snake activity data is completed, we will determine the relationship between activity and predation rate.

30

DAILY ACTIVITY PATTERNS OF FREE-RANGING, GREAT BASIN RATTLESNAKES. V.A. Cobb and C.R. Peterson, Idaho State University, Pocatello, ID.

Although there have been numerous studies of snake movements, there are few data describing the daily (24-hour) activity patterns of individual, free-ranging snakes. To determine the effect of environmental and body temperatures on the daily activity patterns of snakes, we captured four, adult Great Basin Rattlesnakes (*Crotalus viridis lutosus*) near their denning area on the Idaho National Environmental Research Park in late spring of 1990. We then surgically implanted radiotransmitters equipped with temperature and motion sensors into the snakes and returned them to the field in early summer. Thermal conditions were measured with copper snake models, thermocouples, and a datalogger. We used portable, recording telemetry systems to sample the body temperatures and activity levels of two snakes every six minutes for up to three days at a time. Preliminary data analysis suggests: (1) a bout of activity in the morning associated with emergence (e.g., at 0700 hrs), with little activity during the heating phase, often followed by high activity levels in mid morning (0800-1000); (2) little or intermittent activity during the late morning and afternoon, presumably because of high environmental temperatures; (3) a period of moderate activity sometime in the evening (1800-0100); and (4) little or no activity during the night and early morning (0100-0600), possibly because of low environmental temperatures.

31

THERMAL ECOLOGY OF HIBERNATION IN GREAT BASIN RATTLESNAKES. C.R. Peterson and V.A. Cobb, Idaho State University, Pocatello, ID.

Although many species of snakes spend a considerable amount of time hibernating, surprisingly little is known about body temperature (T_b) selection during this period. To measure body temperature variation and associated movements during hibernation, we surgically implanted temperature-sensitive radiotransmitters into seven, adult Great Basin Rattlesnakes (*Crotalus viridis lutosus*). We captured the snakes in September of 1989 at a den site in the desert on the Idaho National Environmental Research Park in southeastern Idaho and released them by mid October. Body temperatures were measured once per week and environmental temperatures were measured every 30 minutes using thermocouples and a datalogger. Most of the snakes entered hibernation during late October and all were hibernating by mid November. Mean body temperatures decreased from approximately 12°C in mid November to a minimum of 6°C in late February and then increased to approximately 7.5°C by late April. The lowest T_b experienced by any of the snakes was 4.2°C. During the winter, differences in T_b's among individuals measured at the same time were as great as 4°C. Dates of emergence ranged from May 4th to May 22nd. These results indicate considerable interindividual variation in body temperature selection by hibernating snakes. We currently are investigating the consequences of this variation and its relationship with the physiological condition of individual snakes.

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RECOVERY OF PLANT SPECIES ASSOCIATIONS IN THE AREA IMPACTED BY THE MOUNT ST. HELENS VOLCANIC ERUPTION. W.H. Emmingham and J.A. Entry, Oregon State University, Corvallis

Abstract

Long-term forest succession studies were initiated in mature undisturbed forest communities prior to the eruption of Mt. St. Helens. These plots were relocated to identify changes in plant associations following the eruption. The damage to plant communities ranged from total destruction and complete burial to minor effects of being coated with fine ash.

Ten years after the eruption, the vast majority of plant species that were affected by blast or tephra deposition do not occupy the amount of ground area that they did prior to the eruption. Our data indicate that the recovery process is much slower following a volcanic eruption than a fire or insect epidemic.

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TEN YEAR RECOVERY OF FOREST VEGETATION IMPACTED BY THE MOUNT ST. HELENS ERUPTION. J.A. Entry and W.H. Emmingham Oregon State University, Corvallis.

Abstract

Forest succession studies were initiated prior to the eruption of Mount St. Helens in mature undisturbed forest communities. We compare species cover estimates for 10 years after the eruption with pre-eruption values among 5 different types of volcanic disturbance: and forests that received < 5 cm, 6-10 cm, 11-25 cm of blast zone tephra mudflows.

We compared species cover estimates for 10 years after the eruption with pre-eruption values. In the blast and mudflow areas species richness and cover remained depressed ten years post-eruption. Up to 25 cm of tephra deposit did not affect the cover of mature or regenerating trees significantly. As little as five cm tephra reduced bryophyte cover significantly, and higher levels of deposition (11-25 cm) significantly affected both herb and shrub cover.

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MOVEMENT OF RADIO TRANSMITTERED PARAFFIN DIPHACINONE BAIT BLOCKS BY FOREST POCKET GOPHERS (THOMOMYS spp.). J.P. FARLEY and D.L. CAMPBELL, USDA APHIS S&T, Denver Wildlife Research Center, Forest Animal Research, Olympia, WA.

The fate of bait blocks (EPA Reg. No. 56-57) designed for long term control of pocket gopher damage to conifers is being evaluated in southern Oregon. Six gram radio transmitters were embedded in 31 bait blocks (10.5- x 4.5- x 3 cm) on two study units. Blocks (129 g) fit tightly in 15 cm deep active burrows in 26 pocket gopher burrow systems. Transmitters were attached to 12 pocket gophers (8♀ and 4♂) in these systems; animal weights averaged 72.3 g (63 g to 80 g). Bait blocks and gophers were monitored for about 56 days. Transmitters/bait blocks were repeatedly moved by pocket gophers. Transmitters or bait were recovered from burrows (57%), food caches (30%), nests (7%), and above ground (6%); one was not recovered. Movement averaged 8.7 m to food caches, 3.2 m to nests, and 7.9 m in burrows; maximum movement was 28.2 m. Average recovery depth was 0.5 m and the deepest was 0.9 m. Thirteen percent of the blocks remained whole or partly chewed. Overall, 84% of the bait blocks were moved.

35

Prehistoric Land Use of the Snake River Plain. M.G. Plew, Boise State Univ., Boise.

This paper presents an overview of findings relating to the early settlement and utilization of the Snake River Plain with reference to new data and theories pertaining to emmigration to the Americas. The results of investigations which suggest long term use of water related resources are presented, noting apparent economic shifts of the past 10,000 years.

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GERMINATION AND PROPAGATION OF MEADOWFOAM (LIMNANTHES) FROM HALF SEEDS. D.SOUTHWORTH AND S.KWIATKOWSKI, SOUTHERN OREGON STATE COLLEGE, ASHLAND.

A method for selecting high oil-producing lines and for propagating particular genotypes has been developed. Seeds of meadowfoam (Limnanthes sp.) were cut transversely or longitudinally. A germination rate greater than 90% was obtained. Seeds cut transversely across the cotyledons gave the most uniform plant establishment. Imbibition to soften the seed before cutting reduced germination. Half seeds could be stored frozen for up to one month with no loss in germination potential. Meristems of established plants were brought into culture, and cultured meristems were cloned into seven to ten plants. The use of half seeds makes available a wider range of selection possibilities for meadowfoam.

Supported by NSF Grant DCB 8801902.

37

OAK LICHENS IN REDWOOD NATIONAL PARK. W.C.Denison, Oregon State Univ., Corvallis.

Oregon White Oak (Quercus garryana) is host to a rich flora of epiphytic lichens. Some lichen species occur wherever the oak is from northern California to B. C. The presence or absence of others depends on climate, air quality, or fire. The Oregon White Oaks in the Bald Hills of Redwood National Park have many of the same lichens found on oaks to the north. Use of fire to encourage the oaks may threaten their lichen populations.

38

AN ELECTRICALLY DETONATED DOWNHOLE SEISMIC GUN. J. C. Parker, J. R. Pelton, M. E. Dougherty, Department of Geology and Geophysics, Boise State University, Boise, Idaho.

An electrically detonated downhole seismic gun (EDG) that will operate under water has been constructed and tested to 30 meters depth. Although other engineering seismic guns are available, they are for near-surface shots and cannot be used for downhole seismic surveys in water-filled boreholes. The EDG was designed primarily for well travel-time surveys and high-quality noise tests, but potential applications include shallow vertical seismic profiling and borehole to borehole or borehole to surface tomography, as well as optimum offset and common midpoint seismic reflection surveys. The EDG consists of four steel subassemblies: (1) chamber; (2) breech; (3) pipe; and (4) hanger. A blank 8-gauge electrical shell is held by the chamber and is detonated by an electrode located inside the breech. The breech and electrode are surrounded by o-ring seals and nylon insulators to prevent water from causing short circuits. The breech is screwed into a 2" schedule-160 black pipe which is also fitted with o-ring seals to keep the internal wiring dry. The hanger contains a bulkhead connector to tie the surface electrical cable to the internal wiring. A clevis pin attaches aircraft cable to the hanger so that the EDG may be lowered and raised within a deep borehole. Arming of the EDG with a blaster occurs only after lowering to operating depth. The EDG can currently be used with any size black powder load up to a 500-grain maximum. Tests for frequency content and repeatability are in progress.

39

COLONY FOUNDING IN HARVESTER ANTS: ENVIRONMENTAL CONSTRAINTS. J.C. Munger, Boise St. Univ., Boise, ID.

I conducted experiments to determine the effect of temperature and water potential on survival and reproductive success of harvester ant queens. Newly mated queens were captured and randomly assigned among 24 treatments consisting of all possible combinations of 5 temperatures (25, 30, 35, 38, and 40°) and six water potentials (-125, -250, -500, -1000, -2000, and -4000 kPa) At higher temperatures, survival was low; the maximum temperature that can be survived for prolonged periods is $\geq 35^{\circ}$ and $< 38^{\circ}$ C. Although queens laid eggs at 25-38°, only those at 30-35° developed into workers. Water potential may be limiting as well. No workers were raised at water potentials of -125 kPa (most moist) or at -4000 kPa (driest). Future field studies will determine if there are areas which cannot be colonized because of inappropriate temperature and water potential regimes.

40

DEEP SUBSURFACE MICROBIOLOGY FIELD STUDIES IN SE IDAHO AND SE WASHINGTON: PRELIMINARY RESULTS AND COMPARISONS. T.O. Stevens, S.W. Li, F.J. Brockman, and J.K. Fredrickson. Battelle, Pacific Northwest Laboratory, Richland, WA.

Dedicated boreholes were dug for coordinated microbiology and geochemistry studies as part of the DOE Subsurface Science Program. The Idaho borehole sampled basalt flows with sedimentary interbeds (233K - 600K years old) through the unsaturated zone and into the Snake River Plain Aquifer to a depth of 182 m. The Washington borehole sampled suprabasalt sediments (up to 4 M years old) through the unsaturated zone and into the Hanford Unconfined Aquifer to a depth of 102 m. Multiple tracer systems ensured that samples were not contaminated from the surface or from drilling procedures. Deeper (1800 m) confined aquifers were also sampled through artesian wells. Microorganisms were detected and characterized by microscopic observation, plate counting, enrichment culture, and activity measurement techniques. Unsaturated basalt flows and catastrophic flood deposits were generally devoid of life, while significant, viable bacterial populations were detected in unsaturated paleosol formations. Saturated zones contained relatively large populations, even within basalt formations. The deep confined aquifers contained large anaerobic bacterial populations. Geochemical data was correlated with microbiological data to explain these trends.

41

ECOSYSTEMS AND POLITICAL SYSTEMS: PROBLEMS IN INTEGRATION. John C. Freemuth, Boise State University, Boise.

One of the most interesting new ideas in natural resource management is ecosystem management. Ecosystem management centers on the administration and management of large areas as integrated ecosystems, attempting to overcome traditional jurisdictional boundaries created at an earlier (and implicitly more ignorant) time. Yet established agency values, as well as ongoing political traditions and decision systems, may render the implementation of ecosystem management problematic. This paper explores the relationship between the ecosystem and the political system, as well as obstacles which have to be overcome to integrate these two approaches to land management decisionmaking.

42

SCIENCE AND LAND USE ON THE BOISE FRONT: A PLACE FOR SCIENTIFIC ACTIVISM IN CITY PLANNING?
Gary Richardson, Idaho Conservation League, Boise

Actual and potential uses of science in informing the city planning process are discussed.

Anecdotal observations of citizen efforts to affect land use decisions in the Boise foothills illuminate possible roles for science in urban land use policy.

In many cases, the injection of science into local public policy debate is the privilege of those who can afford it and is, therefore, very selective and not particularly disinterested.

There is an important role for the application of scientific information and scientific methods to urban land use planning and management. Activism by those trained in the relevant social and environmental sciences is needed if scientific knowledge is to affect these important public policy directions.

43

SMALL SCALE SEISMIC SCATTERING IN OCEAN CRUST, AS SEEN IN OSE DATA FROM SITE 418A. R.J. Vincent, M.E. Dougherty, Boise State University, Boise, Idaho, and S.A. Swift, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

Scattered arrivals seen in seismic data collected from an oblique seismic experiment (OSE) located on the Bermuda Rise (100 m.y. old crust) are used to examine the small scale lateral variability of the upper oceanic crust. An OSE explores the crust surrounding a borehole seismic receiver, providing information on the structure at various depths and directions around the borehole. A three component receiver (three orthogonal directions) placed at several depths below the ocean floor records one vertical and two components of motion. This gives a better description of the arriving waves than a single component receiver. Computer models were created to replicate effects of randomly distributed heterogeneities in the upper ocean crust on first arrivals and coda. Finite difference modelling is used because of the relative ease of setting up a model, and a more complete description of the wave propagation is calculated compared to other methods. Wave forms, spectra, and arrival times are checked between synthetic and field data to determine adjustment of the seismic model parameters. Preliminary results suggest examination of spectral properties for both arrivals and coda can be used to deduce some statistical properties of the small scale heterogeneities in the crust.

44

MONITORING FOR IMPACT OF INEL ON THE SNAKE RIVER PLAIN AQUIFER. W. Barrash, Idaho Dept. Health & Welfare, Boise

The Idaho Legislature in 1989 created the INEL Oversight Program to provide independent, thorough, factual analysis of the environmental and public health features and impacts of all present and proposed INEL activities or projects. The SRPA has been monitored by INEL-related entities for 40 years; now the Idaho program is reviewing and evaluating current and historical monitoring both on- and off-site. Also the State will conduct vertical profiling in the SRPA and assessment of water and contaminant transport through the unsaturated zone in cooperation with Idaho universities and the Idaho Geological Survey. State review of INEL-related SRPA contamination to date indicates: very low activities of tritium and Cl-36 have passed beyond, but not far from, the southern boundary of INEL; no contamination has been detected between the region near the southern site boundary and Hagerman; and tritium and TCE have exceeded MCLs in two drinking water systems at INEL. Contamination of the SRPA at INEL with Sr-90, I-129, Cr, CCl_4 and other species are being monitored or investigated.

45

THE ROLE OF LICHENS IN THE ECOLOGY OF THE NORTHERN FLYING SQUIRREL. Roger Rosentreter, Bureau of Land Management, Boise, ID.

Lichens play an important role in the trophic dynamics of old growth forests. Evidence from this study show that arboreal lichens are important as food and shelter for the northern flying squirrel, especially during the winter. Flying squirrels are part of the diet for forest dwelling owls. Forest practices that destroy and hinder the recolonization of lichens threaten both lichens and forest dependent animals. Squirrels eat lichens rather than other foods in the winter because they: 1) are the only source of free water, 2) are free of toxins, 3)contain some nitrogen, 4) are easily digestible, and 5) are available above the snow.

46

ENERGY BALANCE OF SAGEBRUSH-GRASS RANGE SITES. C.L. Hanson and J.R. Wight, USDA-ARS, 800 Park Boulevard, Plaza IV, Suite 105, Boise, ID 83712.

We used the Bowen ratio method to determine the energy budget at three rangeland sites on the Reynolds Creek Experimental Watershed in southwestern Idaho. The sites were similar in vegetational cover but varied in elevation between 1402 and 2097 m; and the annual precipitation varied between 300 and 700 mm. Early in the season, at the times of day when maximum evapotranspiration (ET) occurred, ET accounted for 25, 33 and 36 percent of the net radiation at the low, mid and high elevation sites, respectively. By the end of July, ET accounted for about 6 percent of the net radiation at the two lower elevation sites and 30 percent at the high site. Sensible heat flux to the air was computed as the difference between net radiation and latent heat flux (ET), plus sensible heat flux to the ground. The effects of daily weather and site characteristics on partitioning of available energy are also discussed.

47

FOLIAR INITIATION AND THE FATE OF THE DWARF-SHOOT APEX IN PINUS MONOPHYLLA Emerenciana Hurd and H. Lloyd Mogensen, USDA, Forest Service, Forestry Sciences Laboratory, Boise, ID and Northern Arizona University, Flagstaff.

The dwarf-shoot apex of Pinus monophylla has a cytological zonation typical of pines. Cataphylls are initiated by the apex both before and after the dormant winter period. The needle is initiated in the spring of the same season in which it matures. The cytological details of cataphyll initiation are identical to those of needle initiation. However, the two primordia can be distinguished very early on the basis of their shape and direction of growth. After needle initiation the stem apex becomes inactive, is crowded to one side, and eventually disappears as the base of the needle enlarges. The results of the present work are discussed in relation to earlier conflicting interpretations regarding needle initiation and the subsequent existence of the dwarf-shoot apex of P. monophylla.

48

BEHAVIOR OF NESTING PRAIRIE FALCONS (FALCO MEXICANUS). A. M. A. Holthuijzen, Idaho Power Co., Environmental Affairs Dept., Boise, ID 83707.

From 1984 through 1987, 52 prairie falcon nesting attempts were observed in southwestern Idaho for 613 days. Observations were made from sunrise to sunset. Nest sites were observed during preincubation (91 days), incubation (267 days), and brood rearing (255 days) until young were 35 days. Mated pairs occupied nest sites and copulated at least 5 weeks prior to egg laying. Eggs were incubated 97% of the day after the 1st week of incubation, mostly by the female (63%). Females usually incubated at night. Brooding, mainly by the female, declined from 89% at hatch to 8% when the young were 15 days. The female brooded young at night until they were 21 days. The proportion of the day a pair was absent from the nest site 4 weeks prior to incubation averaged 22%, but decreased rapidly to 2% during early incubation. A rapid increase in pair absence from the nest site was found during brood rearing from 1% just after hatch to 27% when young were 35 days. Males delivered 76% of all prey. Prey delivery rates by male falcons were about 4 times higher during brood rearing than during either preincubation or incubation. During preincubation males spent 63% of the day away from the nest site, declining to 42% during incubation, but increasing once more to 63% during brood rearing. In contrast, females spent 15% of the day away from the nest site during preincubation and incubation, but 54% during brood rearing.

49

HYDROLOGY OF THE WESTERN SNAKE RIVER PLAIN, IDAHO. G.F. Lindholm, U.S. Geological Survey, Boise.

Hydrology was described as part of a regional aquifer study of the Snake River Plain. The major hydrologic control is the Snake River. Fine-grained, unconsolidated Quaternary and Tertiary rocks as thick as 5,000 feet predominate. They overlie Tertiary volcanic rocks that yield geothermal water along the margins of the plain. Alluvium and terrace gravels in the Boise River valley and basalt in the Mountain Home area are major aquifers. Ground-water levels are declining in several areas because of increased pumping, changing irrigation practices, and prolonged below-normal precipitation. Precipitation deficiencies have resulted in decreased flow in the Boise and Snake Rivers. In 1980, nearly 400 pumping stations withdrew 550,000 acre-feet of water from the Snake River. Water-budget analysis indicated that a total of 16.5 million acre-feet of water moved through the western plain in 1980. The Snake River and tributary basins each accounted for about 40 percent of inflow; the remainder was precipitation on the plain. About 1.7 million acre-feet of water moved through the ground-water system. Irrigation

50

A REAPPRAISAL OF THE MORPHOLOGY OF LOMATIUM COUS (S. WATS.) COULT. & ROSE (APIACEAE) FROM HIGH ELEVATIONS. K.S. Antell, Eastern Oregon State College, La Grande.

The objective of this study was to quantify the morphological differences between high and low elevation plants of Lomatium cous and to clarify the differences between these and other, similar high elevation Lomatium taxa. Specimens of L. cous collected from both above and below 9,000 ft. elevation were evaluated for eighteen morphological characters. The computer program NTSYS-PC was used to generate a phenogram and individual characters were plotted against elevation. The most discerning characters for discriminating between high and low elevation plants were pedicel and ray length, root width and plant vestiture. Lomatium cous plants from above about 9,000 ft. elevation had a suite of morphological characters distinct from all other plants.

51

SUSCEPTIBILITY OF LODGEPOLE PINE FROM THE MIDDLE COLUMBIA RIVER SYSTEM TO WESTERN GALL RUST. R.J.Hoff, USDA Forest Service, Intermountain Research Station, Moscow, Idaho

Two-year-old lodgepole pine seedlings from 107 provenances were artificially inoculated with one source of western gall rust. Average level of infection was high; 87 percent had galls two years after inoculation. Stepwise multiple regression indicated a weak relationship between number of galls per tree and latitude and elevation of the provenance. Relationships between the degree of infection and mortality of diseased trees varied with provenance but displayed only random variation with geography and elevation. Some provenances were highly resistant, with over half of the seedlings showing no galls. Three symptoms of resistance were noted. One, the absence of galls and necrotic reactions in the stem. Two, presence of necrotic reactions in the stem. Three, death of galls resulting in disease free trees. Selection programs with objectives of improving the growth and quality of lodgepole pine should include resistance to gall rust in their selection programs.

52

THE EFFECTIVENESS OF UROPHORA AFFINIS AND U. QUADRIFASCIATA IN REDUCING SEED PRODUCTION IN KNAPWEED SPECIES. Ronald J. Taylor and Richy J. Harrod, Western Washington Univ., Bellingham.

Mature seed heads were collected from populations of knapweed species: Centaurea diffusa, C. maculosa, C. repens, and C. solstitialis. As was expected, no galls were formed in heads of C. repens and C. solstitialis. Galls of both Urophora affinis and U. quadrifasciata were formed in the other two knapweeds. Various correlation analyses were carried out to determine the relationship between seed production and type, presence and number of insect galls. Although the results were complicated by other factors influencing seed production, there was a significant negative correlation between gall numbers of both fly species and seed numbers. However, the reduction in seed numbers was not deemed sufficient to reduce population density. The occurrence of U. affinis galls had a greater (negative) effect on seed production than did that of U. quadrifasciata. Interestingly, there was a significant negative correlation between the numbers of galls of the two fly species when they occurred together in seed heads. This suggests that under sympatric conditions, U. quadrifasciata may actually promote seed production through competition with and displacement of the more destructive U. affinis. Finally, interesting distributional information of the two Urophora species was obtained.

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POLLINATION ECOLOGY OF CENTAUREA DIFFUSA LAM.(COMPOSITAE). Richy J. Harrod and Ronald J. Taylor, Western Washington Univ., Bellingham.

An experiment was designed using cages and transects to determine the mode of reproduction and pollination of *Centaurea diffusa*. Importance of various insects as pollinators was determined by visitation frequency and pollen load analysis. Major pollinators, *Apis mellifera*, *Anthophora* sp. and *Bombus* spp., did not discriminate between white- or purple-flowered plants. Time of day did not significantly influence visitation, except for *Anthophora* sp. which visited primarily in the morning. A small amount of pollen was transported by wind. *Centaurea diffusa* was found to be an obligate outcrosser. Seed set in white- and purple-flowered plants was compared; 30% more were produced by purple plants. Nectar in both color morphs consisted of a 2:1 ratio of sucrose to fructose.

54

PLANT COMMUNICATION REVISITED. O.E. Wagner. Wagner Research Lab. Rogue River, OR 97537.

Factors important to observation of direct communication are as follows: (1) Choose a low noise time of year. Early spring may be the best time when insect activity in vivo is at a minimum. Electrical activity also tends to be at a lower level. (2) Choose tree trunks that are relatively free of branches so that reflection peaks are minimized. (3) Electrodes need to be spaced far apart since it appears that signal strength is proportional to the square root of the spacing. It is not clear whether communication can be easily demonstrated in smaller plants because the electrode spacing is limited. (4) Detection equipment should be of the low noise variety. For additional hints and methods see the book by the author "W-waves and a Wave Universe". Plant structure and obvious plant-gravity effects may indicate that there is a difference between vertical and horizontal W-wave velocities in air and perhaps even in the plant. The gravitational field may strongly influence W-wave velocities with lower velocities in higher gravitational fields with resultant effects on plant communication etc.

55

W-WAVE SOLUTIONS FOR PLANETARY RINGS. O.E. Wagner. Wagner Research Laboratory, Rogue River, OR 97537.

The sun appears to oscillate at a frequency of about 1/22.2 years (solar cycle). This also is a frequency of $1/r_o$, where r_o is the radius of the sun in meters(note that the 1 in $1/r_c$ apparently indicates a velocity of 1 m/sec consistent with measured W-wave velocities in matter). Next assume that the gaseous planets also oscillate at a frequency of $1/r_o$ where r_o is the planetary radius. It is conjectured that gaseous planets are layered. Layer boundaries (and differences in layer composition) would represent discontinuities and produce reflections resulting in additional oscillation frequencies. The orbit equation ($r=r_o \exp(0.625N)$) applied to satellite locations, the velocity equation ($v=1.25\exp(0.625N)$), and the derived ring frequency equation ($f = 1.73/(r-r_o)$) reveal discontinuity locations. Difference frequencies from the heterodyning of planetary frequencies appear to explain the rings and ring structure in a consistent manner (see the book "W-waves and A Wave Universe" by the author). I will solve the ring system of Neptune as time permits.

56

GEOLOGY OF THE WESTERN SNAKE RIVER PLAIN. D. M. Gallegos, Boise State Univ., Boise, Idaho

The Western Snake River Plain (WSRP) is a structural trough, bounded by normal faults, that lies at the juncture of several tectono-magmatic provinces. Up to 2 km of Neogene lake and river sediment underlies the WSRP. Many lakes likely existed during the evolution of the basin; one such large lake is referred to as the Pliocene (1.6 -.1 Ma) "Lake Idaho". Evidence for a lake level high stand of 1150 m exists on both sides of the WSRP. The upper portion of the Neogene sedimentary and volcanic rocks is well exposed in the Boise foothills along the northwest margin of the WSRP where they are cut by a complex network of faults. Facies distribution along the basin margin allows identification of sedimentary cycles that reflect lake level fluctuation. This basic geologic data impacts land development planning and the prediction of fluid migration with respect to ground water resources, contaminant flow and the geothermal system.

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HOME RANGES AND FORAGING HABITAT OF OSPREYS (PANDION HALIAETUS) AT CASCADE RESERVOIR, IDAHO. J.M. Phelps III and M. J. Bechard, Raptor Research Center, Department of Biology, Boise State University, Boise, Idaho 83725.

This study described physical features important to osprey foraging habitat. Four male ospreys were trapped, fitted with radio transmitters, and followed throughout the nesting season to determine home ranges and physical features of foraging habitats. Preliminary results indicated that factors of most importance were those affecting prey (fish) availability such as water depth, clarity and distance to shore. The study will continue in 1991 to determine how the factors affect prey availability and hunting success.

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THE POLLINATION ECOLOGY OF SILENE ACAULIS (CARYOPHYLLACEAE). Frank R. Borzager and Ronald J. Taylor, Western Washington Univ., Bellingham.

This study was conducted in the summer of 1989 in an alpine fell-field on Chowder Ridge, near Mt. Baker, Washington. Silene acaulis is a gynodioecious species and data were collected from both female and hermaphrodite plants. Cages were used to exclude insect pollinators from selected plants. Importance of various pollinators was determined by visitation frequency and pollen load analyses. Individuals of the family syrphidae were found to be the most important pollinators. In addition, flower sizes and seed and nectar production were measured. Corolla-tube width and length and corolla-limb width of pistillate and perfect flowers were found to be significantly different. Pedicel length was not significantly different. With one exception, caged hermaphrodite plants produced no seeds. Open-pollinated female plants tended to have more capsules than did hermaphrodite plants. Pistillate flowers produced significantly more nectar than perfect flowers. Pistillate flowers produced a glucose/fructose-rich nectar while perfect flowers produced a sucrose-rich nectar.

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THE EFFECTS OF HABITAT PATCHINESS ON THE SPATIAL DISTRIBUTION AND SOCIAL ORGANIZATION OF MICROTINE RODENTS. L.E. Mackelburg and J.G. Hallett, Department of Natural Resource Sciences, Washington State Univ., Pullman, WA 99164-6410

A population of Microtus montanus (montane vole) was monitored before and after habitat modification of determine the effects of habitat patchiness on the demography, spatial distribution, and social organization. The population was to October 1990 on a vegetatively homogeneous grid (3.5 ha) dominated by Poa and Agropyron grasses. In June 1990, the grid was mowed to create 18 habitat patches of three different sizes ($144m^2$, $216m^2$ and $288m^2$). Analyses of population size, residency, rate of recruitment, home range size, and co-occurrence were used to examine the effects of habitat patchiness. The minimum number alive per patch tended to increase with patch size. Home range size for both sexes was reduced after habitat modification. However, territorial males were more affected by the reduction in available habitat than were females. This study provides insight into the interrelationship of resource distribution and social organization of microtine rodents.

60

NICHE OVERLAP OF NORTHERN SHRIKES (LANIUS EXCUBITOR) AND AMERICAN KESTRELS (FALCO SPARVERIUS) WINTERING IN SOUTHWEST IDAHO. E.C. Atkinson, Boise State Univ., Boise, ID.

The niche positions of Northern Shrikes and American Kestrels were described where they winter in sympatry. Their positions were described in reference to five major resource axes: Macrohabitat association, Perch height, Vegetation surrounding hunting perches, Diet (by item), and Diet (by biomass). Overlap values (α) were greater than 0.83 on all axes but diet (by item) which may be partially explained by the diversity of shrike prey choice and by kestrels specializing upon microtines. Logistic regression produced a model to predict the probability of perch use by shrikes based upon the amount of shrub cover and perennial grass surrounding the perch. This equation correctly classified 81.25 and 75% of the shrike and kestrel perches, respectively while accounting for only 22% of the variance. Factor analysis of vegetation surrounding perches showed that of the three factors accounting for 100% of vegetative variability separation of the species was only evident on factor 3 ("riparian-ness"). High niche overlap may provide motivation for interspecific territoriality between these species.

61

THE BACON STREET LANDSLIDE, AN ANALYSIS OF SLOPE FAILURE. Justin Bolles, Boise State University., Boise.

Lacustrine and fluvial sediments exposed in the Boise foothills are extensive and widespread and pose a risk for land developers. This material is unstable and may contribute to slope instability. Various landslides have occurred within the Boise area; the Bacon Street landslide, began to move in the Spring of 1983. As of 1990, this slide had not caused any property damage, but it is alarmingly close to a residential subdivision. The slide is believed to have been initiated by water oversaturation of the substratum during 1983, which was one of the wettest years of the previous decade. The chance for reactivation due to heavy precipitation is large and would be potentially threatening. Proper management and assessment is the key to avoiding mass-wasting disasters.

62

LICHENS AS BIOINDICATORS OF AIR QUALITY ON THE TONGASS NATIONAL FOREST. C.C. Derr and L. Geiser. Oregon State Univ., Corvallis.

The U.S. Forest Service has established permanent plots to monitor air quality on the Tongass National Forest in Southeast Alaska, using lichens as bioindicators. Plots were established in Pinus contorta/Sphagnum bogs and Tsuga heterophylla old growth, in areas considered to be representative of pristine baseline conditions throughout Southeast Alaska. Tissue samples of four lichen species, Lobaria oregana, Alectoria sarmentosa, Cladina rangiferina and Hypogymnia enteromorpha were collected at over 80 sites and sent for analysis to determine current tissue concentrations of sulfur and 15 other elements. Baseline lichen community data is being analyzed for comparison with communities whose structure may become altered due to anthropogenic air pollutants in the future. Distribution maps and a species inventory are being prepared for the Tongass.

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COMMUNITY PATTERNS ALONG A WATER LEVEL GRADIENT IN FRESHWATER WETLANDS. Michael Emers, College of Forest Resources, University of WA.

Percent cover of plant species and above ground biomass were examined in the transition zone between annual high and low water in six herbaceous freshwater wetlands in western Washington. Objectives were to characterize transition zone vegetation ; investigate similarities among sites of differing annual water fluctuations; examine within-site pattern of species associations and richness at different elevations between high and low water. Where it was hypothesized that aspects of hydroperiod were the primary factors influencing associations and diversity patterns, results of multivariate analysis and comparisons of diversity, biomass, and elevation above low water showed that within-site factors were more important. Species associations observed were diverse groups characterized by *Juncus acuminatus*, *J. supinus*, *Ludwigia palustris*, *Lycopus unifloris*, *Sparganium emersum* and *Veronica scutellata* and more monotypic associations dominated by *Phalaris arundinacea* and *Typha latifolia*. These associations were more site specific rather than related to elevation. Most often within-site richness decreased and associations became more similar at lower elevations. In general, the presence of clonal dominants, such as *Phalaris* and *Typha*, was the primary factor influencing associations and patterns.

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VOLCANISM AND FAULTING OF THE EASTERN SNAKE RIVER PLAIN: NEW IDEAS AND IMPLICATIONS FOR GEOLOGIC-HAZARDS ASSESSMENT AT THE IDAHO NATIONAL ENGINEERING LABORATORY
W.R. Hackett, R.P. Smith, INEL, EG&G Idaho, Inc., P.O. Box 1625, Geosciences MS 2107, Idaho Falls, ID 83415

Ongoing INEL geoscience research has led to important new data and interpretations, concerning the interplay of volcanism and tectonism on the Eastern Snake River Plain (ESRP). The integrated results of neotectonic and volcanic field studies, subsurface stratigraphy, geophysical modeling, and geochronology have implications for evolution of the ESRP as a volcano-tectonic basin, and for geologic-risk assessment at INEL facilities. Volcanic rift zones of the ESRP are aligned NNW, parallel to normal-fault trends in the surrounding Basin and Range Province. Geomorphic and geophysical features of ESRP volcanic rift zones are similar to those of active rifts in Iceland and Hawaii, and include linear ground-deformation as well as volcanic features. The surrounding Basin and Range Province responds to regional extension by normal faulting, but extension of the ESRP is accommodated by dike injection: we interpret ESRP volcanic rift zones as manifestations of subsurface basaltic dikes, rather than as continuations of normal faults from the surrounding Basin and Range Province. Dilation of dike walls due to magma pressure keeps ESRP deviatoric stresses low (Thompson *et al.*, 1990) and prevents development of tectonic normal faults. Historical data from active rifts elsewhere show that dike injection is either aseismic or involves earthquakes of M<4. Thus, extension by dike injection is consistent with the low deviatoric stresses, relative aseismicity and absence of normal faults on the ESRP, in contrast to the surrounding Basin and Range Province.

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SEASONAL PHYSIOLOGIC AND COMMUNITY RESPONSE TO A RIPARIAN MONTANE MEADOW WATER TABLE GRADIENT. G.M. Riegel[1], T.J. Svejcar[2], and J.D. Trent,[1], [1] USDA-ARS, 920 Valley Road, Reno NV 89512 and [2] USDA-ARS, HC 71, 4.51, Hwy 205, Burns, OR 97720.

Many highly productive meadows lose much of their productivity when stream channels become eroded or down cut. Mesic communities that once dominated the meadow may now be restricted to the zone adjacent to a stream. The objective of this research was to determine how a decrease in water table depth caused from down cutting, influences physiology of montane meadow species in the northern Sierra Nevada. We identified three species Carex nebraskensis, Juncus balticus and Deschampsia caespitosa that occur at locations along the wet (adjacent to the stream) to dry (distal) gradient. There were no differences in photosynthesis between wet and dry location though species differences occurred later in the growing season. Transpiration and conductance rates were not different by location but were different between species later in the season. Differences in predawn xylem potentials by location occurred early to mid- season while midday xylem potential differences occurred from early through middle of the growing season. Greater biomass production at the wet site appears to be a function of water table depth and not individual species photosynthetic rates.

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GEOLOGY, LANDFORMS AND LATERAL EROSION OF THE BRUNEAU RIVER. M.G. Butler, Boise State University, Boise, Idaho

An aerial landform study reflects the growth and migration of the Bruneau River in southwestern Idaho. Controls on the fluvial erosion and development of the Bruneau River include lateral migration, lateral accretion, gradient, climate and the geologic history. Lateral migration of the river is a product of sediment type, rates of discharge, gradient and local geologic rock types. Lateral accretion and meander development result from discharge and lateral swing and sweep of the Bruneau River. Bank erosion is responsible for the bulk sediment load and meander development of this active fluvial system. The gradient of the Bruneau is relatively low. The low gradient reflects local geologic characteristics, sediment type, regional folding and Pleistocene erosion. The stability of the Bruneau drainage has allowed for normal fluvial meander processes and landforms to develop.

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INFLUENCE OF ASPECT AND SHADECARDS ON FIRST-SEASON SURVIVAL OF OUTPLANTED DOUGLAS-FIR SEEDLINGS ON A SEVERELY-BURNED SITE IN SOUTHCENTRAL IDAHO. M.H.Jones. Boise State University, Boise, Idaho 83725.

First-season survival of 2-0 Douglas-fir seedlings planted in May 1990 was examined on west to south facing aspects on a severely burned site on Banner Ridge. A total of 220 seedlings were selected from those planted by Forest Service crews, half of which were randomly selected for treatment with standard shadecards. Survival was recorded in September. Significant differences ($P<0.001$) in survival were found between treatments. Control (unshaded) seedling survival was improved with change in aspect from southwest to west. Results of a model regressing control seedling survival on aspect were significant ($R^2 = 0.34$). A datalogger was used to record soil surface temperatures at the root collar and nearby for three seedlings of each treatment type.

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NEIGHBORHOOD ANALYSIS OF NATURALLY-REGENERATED DOUGLAS-FIR SEEDLINGS IN SOUTHCENTRAL IDAHO CLEARCUTS. M.H.Jones. Boise State Univ., Boise, Idaho 83725.

Neighborhood analyses were used to examine survival of Douglas-fir seedlings in clearcuts in the southern Boise National Forest. Microhabitat variables including shade duration and volume of neighboring shrubs by species were recorded for 575 seedling and non-seedling plots over 9 sites. A datalogger was used to record microclimate parameters, including soil surface temperatures. A logistic regression model indicated afternoon shade as the variable most critical to seedling survival, but the model explained only about 15% of the variance. Path analysis was utilized to illuminate relationships between variables. Study results will be used by forest planners to improve natural regeneration on harsh sites.

HOME RANGE AND HABITAT UTILIZATION OF BREEDING MAURITIUS KESTRELS, *FALCO PUNCTATUS*. J. Carter, Boise State Univ., Boise, Idaho.

The Mauritius Kestrel is a forest dwelling falcon on the island of Mauritius where only 6% of the island's original forest remains. This study examined the size of kestrel home ranges in areas of degraded habitat, and the extent to which various habitat types were utilized. Three individuals were monitored by radio telemetry during various stages in the breeding cycle. Home range sizes ranged from 0.79 km^2 to 1.61 km^2. Habitat types found within the home ranges included lowland native forest, mixed exotic woodland, agricultural areas, riparian areas, and monotypic stands of exotic plant species. Mixed exotic woodland and agricultural areas were found to be used significantly more than expected, and lowland native forest was found to be used less than expected ($p<0.05$). These results suggest that the kestrels are adapting to non-native habitat types.

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OUTSTANDING SCIENTIST AWARD

NORTHWEST SCIENCE

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Announcements

Outstanding Scientist Recipient for 1990: James N. Trappe

Recognition of The Outstanding Scientist presented by Northwest Scientific Association was awarded to James N. Trappe. He received academic degrees at the University of Washington (B.S. in Forestry, 1954), State University of New York at Syracuse (M.F., 1956), and again at the University of Washington (Ph.D. in Forestry, 1962). He worked for the U.S. Forest Service, Pacific Northwest Research Station, from 1956 to 1986. Since 1986 he has been Professor of Forest Science and of Botany-Plant Pathology at Oregon State University. Professor Trappe's research has focused on mycorrhizae and taxonomy of mycorrhizal fungi. He has authored or co-authored 220 scientific and technical publications and has discovered and named 3 new families, 13 new genera, and 80 new species of mycorrhizal fungi. In addition, he is particularly recognized for his research on ecology of mycorrhizae, use of fungi as food by mammals, and the role of fallen trees in forest ecosystems. He has been invited to give workshops and conduct research in 15 countries, including Argentina, Australia, India, Spain and Sweden. In 1985 he received the "Milestones in Mycorrhiza Research" award from the University of Hannover, Germany.

Professor Trappe was Vice President (1969) and President (1970) of the Northwest Scientific Association, and Vice President (1984) and President (1986) of the Mycological Society of America. He has been active in civil rights activities, having been given civil rights awards by the U.S. Forest Service and, in 1990, the Civil Liberties Award of the American Civil Liberties Union for his active support of First Amendment freedoms of prisoners. He has received 13 major grants from the National Science Foundation and 12 grants from other foundations or agencies.

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Nominations for these two awards should be forwarded, by July 31, to:

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1. The person shall be known nationally or internationally for his/her scientific accomplishments, *or* shall have performed work of outstanding importance to the Northwest.
2. A majority of his/her work shall have been accomplished either while residing in the Northwest, or shall have been performed on Northwestern systems.
3. Preference shall be given to residents whose work is of importance to the Northwest.
4. Preference shall be given to those past or nearing retirement, and to those whose accomplishments have not received sufficient notoriety via other awards.
5. Membership in the Northwest Scientific Association is not a consideration in making this award.

(Announcements, continued on last page)

Dale Toetz and **Maurice Muoneke,** Zoology Department, Oklahoma State University, Stillwater, Oklahoma 74078

and

John Windell, Department of Evolutionary, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80309

Age, Growth and Condition of Brook Trout (*Salvelinus fontinalis*) from an Unexploited Alpine Lake

Abstract

The purpose of this study was to provide baseline data on fish populations in the Green Lakes Valley (Colorado Front Range) as part of the long-term ecological research program of the University of Colorado. While the results were site specific, the fish sampled (brook trout, *Salvelinus fontinalis*) had been unexploited for the past 50 years. Because data from unexploited fish populations are rare, they are presented here for use by fisheries biologists and ecologists who often need to know the potential for fish growth and longevity under unexploited conditions. Fish were sampled with gill nets from Green Lake 3 (GL3) and total length, weight and sex determined. Otoliths were used to estimate age. Females outlived males; the maximum longevity was 13 years. Growth and condition of GL3 brook trout was within the range observed in other studies of the species in western U.S. lakes with one exception. Brook trout from Bunny Lake, California, had a longer life span (24 years), much lower condition and slower growth than GL3 brook trout. These data will be a valuable reference point for those interested in this species in high elevation lakes, especially since the study site will be part of the long-term ecological research network.

Introduction

Long-term ecological research (LTER) is being pursued in a number of biomes to understand how natural ecosystems function so that environmental decisions may have a firm foundation (Callahan 1984). The research reported here was part of a long-term ecological study of the Green Lakes (GL) Valley (Colorado Front Range), undertaken by the University of Colorado LTER program. One objective of the first phase of the study was an inventory of fish populations in the Green Lakes (Figure 1). In an initial survey in 1981, one of us (Windell) found only brook trout, *Salvelinus fontinalis,* in Lake Albion, GL2 and GL3. All three populations have been unexploited for the past 50 years by prohibiting trespass and angling in the Green Lakes valley (Platt 1987). The City of Boulder owns the watershed and trespass laws are a means of protecting the water supply of the city.

Unexploited fish populations are relatively rare, although the exact meaning of the term is subject to different interpretations. For example, is occasional removal by a poacher considered exploitation? Almost all public waters can be expected to contain exploited fish populations, unless they are very remote or are protected by trespass laws such as are in force in the Green Lakes valley. Remoteness and trespass laws seem to qualify the GL3 population as unexploited.

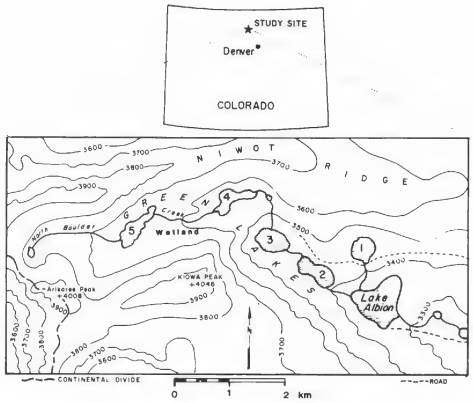

Figure 1. Location map of Green Lake 3.

Unexploited populations are important to ecologists and fisheries biologists because they form a reference point for the study of exploited populations. Angling can be expected to selectively remove larger (older) fish and may alter productivity of different cohorts. In unexploited populations, for example, individuals can be expected to reach maximum longevity.

Brook trout are not native to Colorado and were introduced into the Green Lakes, but no records are available. Brook trout occur in many western North American lakes (MacCrimmon and Cambell 1969) and are often the only fish in alpine

lakes (Donald and Alger 1986) where growth may be stunted (Reimers 1958). In Bunny Lake, California, brook trout live for 24 years, their maximum reported longevity (Carlander 1969, Reimers 1979).

The objectives of this study were to obtain a thorough description of the age, sex ratio, growth and condition of the GL3 population and compare the GL3 population with other higher elevation lake populations of brook trout.

Study Area

Green Lake 3 is located in the Front Range of the Colorado Rocky Mountains at an elevation of 3,455 m in the Green Lakes valley watershed (Figure 1). North Boulder Creek connects GL3 to two fishless lakes upstream, and several lakes with fish downstream, but steep waterfalls prevent immigration. The lake has surface area of 7.5 ha, a mean depth of 8.7 m, and a maximum depth of 15.8 m (McNeely 1984). It does not stratify and has a surface temperature range of 0-11°C (McNeely 1984). The lake level has been artificially raised (date unknown) and the littoral zone contains remnants of peaty soil and dead willows, *Salix* spp. Substrates range in size from sand to large boulders.

Methods

Monofilament gill nets (bar mesh ranging from 10-50 mm) were used to collect fish in 1981. Fish were captured in August, 1985, also using monofilament gill nets (bar mesh 25, 51, and 102 mm) set overnight. On the day of capture all fish were measured (total length, TL) to the nearest mm, weighed (weight, W) to the nearest g, and held at 5°C in a refrigerator. Some of the 1985 fish were dissected, sexed, and otoliths removed shortly after capture. The rest of the fish were frozen and dissected later. Fish whose otoliths could not be found were excluded from subsequent analyses.

Otoliths were cleared in glycerol and age determined using the growth rings on both sagittae (Panella 1974). Otoliths from the same specimen were examined several times if a discrepancy was observed between sagittae from the same specimen. Condition factors (K) were calculated using the expression: $K = W*TL^{-3}*100$.

Scales, not otoliths, were used to age brook trout in the studies cited below. Thus, the following comparisons are done with the understanding that age estimates from otoliths tend to be higher than those from scales in brook trout from high elevation streams (Kozel and Hubert 1987). Further, it is not clear from these literature sources whether the populations were unexploited.

Results and Discussion

The 1985 length frequency distribution suggests selection for larger fish, whereas the 1981 length frequency distribution included smaller fish (Figure 2). Based on the population structure, there is little reason to believe that age distribution was significantly altered by the removal of 106 trout in 1981.

Although sample size is small, females (n = 3) apparently outlived males. The oldest male was 8

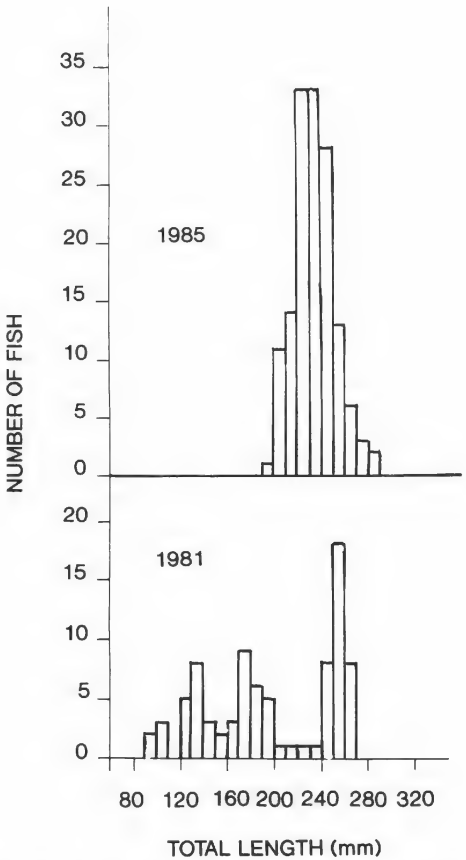

Figure 2. Length frequency histogram of brook trout captured in 1981 and 1985.

years, whereas the oldest female was 13 years (Figure 3). Only four age III trout were captured in the 25-mm mesh, as the gear apparently selected for larger (consequently older) fish. However, the 25-mm mesh was also the only mesh effective for older fish, since the larger mesh sizes captured no fish.

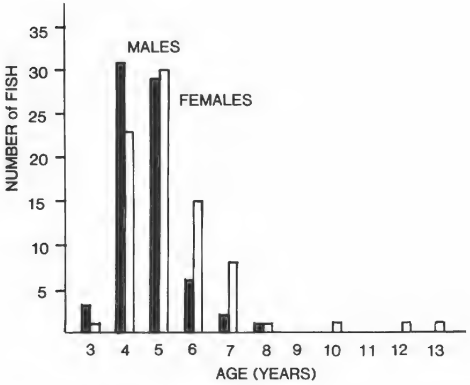

Figure 3. Age frequency histogram of male and female brook trout collected in 1985.

The condition factor of GL3 brook trout was 0.88-1.13 (Table 1) and was not significantly different (paired t-test; $t = 0.17$, $P = 0.88$) between the sexes for fish ages IV-VIII. These values are comparable to those of stunted populations in Colorado beaver ponds (mean 0.99, range 0.63-1.39) (Rabe 1957) and to those in Wyoming lakes (1.03-1.47) (Hepworth 1959) and in alpine Utah lakes (0.80-1.10) (Rabe and Dyer 1964). Maximum longevity is three years in Colorado beaver ponds and five years in Wyoming and Utah lakes.

Where sample size is good there was no significant difference in length between the sexes for fish ages IV-VII (paired t-test; $t = 2.29$, $P = 0.08$).

Comparison of growth of brook trout from four mountain lakes revealed that at ages IV-VI the length of GL3 brook trout is about the same as those from an alpine lake (X-26) in the Uinta mountains of Utah (Rabe and Dyer 1964), and a subalpine lake (Reimers 1958) (Figure 4).

Growth of fish ages IV and V was higher for GL3 fish than for Bunny Lake fish, and the condition factors were also better. For example, at ages IV and V, Bunny Lake brook trout averaged 152 mm and 163 mm TL, respectively (Reimers 1958), whereas brook trout from GL3 averaged 229 and 232 mm (Figure 4). The condition factor of brook trout in Bunny Lake declined from 1.10 to 0.78 in the first six years after stocking, whereas that of GL3 trout between ages IV and VIII was about 1.0.

Perhaps the difference between Bunny Lake and GL3 brook trout population rests in a

TABLE 1. Total length (mm), weight (g), and condition factor for brook trout from Green Lake 3, Colorado, by age group and sex, 1985.

		Length		Weight		Condition factor	
Age	n	Mean	SD	Mean	SD	Mean	SD
Males							
III	3	216	8.7	113	17.1	1.11	0.04
IV	31	231	13.9	132	20.9	1.06	0.09
V	29	243	16.8	148	26.9	1.02	0.11
VI	6	239	11.1	142	11.7	1.04	0.08
VII	2	276		184		0.88	
VIII	1	281		202		0.91	
Females							
III	1	219		119		1.13	
IV	23	229	12.7	123	12.5	1.01	0.07
V	30	232	15.2	126	17.5	0.99	0.10
VI	14	234	11.6	134	15.2	1.04	0.09
VII	8	234	13.5	129	10.1	1.01	0.12
VIII	1	257		141		0.83	
X	1	258		157		0.91	
XII	1	266		153		0.81	
XIII	1	261		135		0.76	

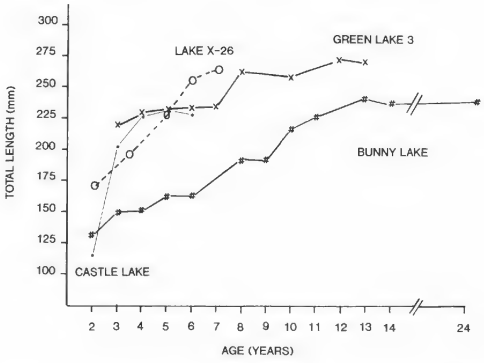

Figure 4. Age and length at capture of brook trout from selected western (US) waters, Bunny Lake, California (Reimers 1958), Lake X-26, Utah (Rabe and Dyer 1964) and Castle Lake, California (Wales and German 1956*).
* = References cited by Carlander (1969).

difference in food supply. Bunny Lake lacks an inlet stream, but GL3 receives an exogenous food supply from lakes above. Drift into GL3 from lakes above is mostly Chironomidae (Mihuc 1987). In a study of 23 Canadian mountain lakes, Donald *et al.* (1980) found that amphipod density was the most important factor affecting trout growth. Thus food supply, not elevation per se, may be the most critical factor in explaining brook trout growth in mountain lakes.

In conclusion, brook trout from GL3 had growth rates and condition factors typical of the species in mountain lakes, with the exception of Bunny Lake.

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Structure of Burrows Used by the Idaho Ground Squirrel, *Spermophilus brunneus*

Abstract

Idaho ground squirrels, *Spermophilus brunneus*, are associated with shallow, rocky soils at most sites in their restricted range in west-central Idaho. These soils may be <50 cm deep above bedrock and water-saturated during early spring. At three sites in Adams Co., Idaho, all burrow systems in a contiguous area were excavated using hand tools. Burrows with nests (nest burrows, n = 7) were 50-121 cm in maximum depth, 700-2600 cm in length, had 3-11 openings, 2-13 branching tunnels, and 1-7 chambers. Burrows without nests (auxiliary burrows, n = 93) were shorter (15-600 cm), shallower (10-45 cm), had fewer entrances (1-8), fewer branching tunnels (0-4), and fewer chambers (0-2) than did nest burrows. Four types of auxiliary burrows were found: 1) partially open burrows under shrubs, 2) burrows excavated under large rocks, 3) plunging burrows that descended to a single chamber, and 4) horizontal burrows similar to shallow pocket gopher burrow systems. Nest burrows were located in small patches of well-drained soils >1 m deep, not in shallow soils; only auxiliary burrows were found on shallow soils. Thus although *S. brunneus* extensively utilized shallow, rocky soils, nest burrows were placed in adjacent areas with deeper soils.

Introduction

Idaho ground squirrels, *Spermophilus brunneus*, are endemic to a five-county area of west-central Idaho. There are two distinct taxa of *S. brunneus*, and the northern form, which is known from only about two dozen isolated demes in Adams and Valley counties, is the subject of this study. These demes are associated with xeric meadows surrounded by coniferous forest at mid-elevations (1150-1550 m) and typically consist of <200 adults (Yensen, in press). These xeric meadows have shallow, rocky, reddish loams or clay-loams derived from decomposing basalt lavas. Mesic meadows nearby have deeper soils and are often inhabited by Columbian ground squirrels (*S. columbianus*).

The Idaho ground squirrel has received little study. Except for its mating system (Sherman 1989), most details of its biology, including burrow structure, are undescribed. Davis (1939) stated that A. E. Borrell found Idaho ground squirrel burrow entrances under rocks and logs at a site near Bear Creek, and this statement has been repeated in faunal and popular works (e.g., Larrison 1967, Burt and Grossenheider 1976, Larrison and Johnson 1981).

Descriptions of the burrow structures of other North American and Eurasian ground squirrels (*Spermophilus*) have been summarized by Howell (1938), Ognev (1947), and Reichman and Smith (1990). Townsend's ground squirrel (*S. townsendii*) and Washington ground squirrel (*S. washingtoni*) are considered the species most closely-related to the Idaho ground squirrel (Nadler *et al.* 1984). Townsend's ground squirrel burrow systems have been described in some detail (Alcorn 1940, Scheffer 1941, Reynolds and Wakkinen 1987, Reynolds and Laundre 1988), whereas Washington ground squirrel burrow systems have been described only briefly (Scheffer 1941). Columbian ground squirrels are sympatric with *S. brunneus*, and their burrow systems have been described in eastern Washington (Shaw 1924, 1926) and Alberta (Young 1990).

Over the past decade we have repeatedly observed *S. brunneus* using burrows in xeric, rocky meadows with <50 cm of soil above basalt bedrock, although they were also occasionally observed in more mesic areas with deeper soils. Soil moisture readings using Bouyoucous soil moisture blocks indicated that these shallow soils were near or above field capacity for several weeks each spring, then dried out rapidly in early summer. Further, during some winters, the soil freezes down to at least 50 cm (J. Dyer, pers. comm.). This study was undertaken to provide a description of *S. brunneus*' burrow systems and to better understand how they live in these shallow soils.

Study Areas

Three study sites were selected to represent a diversity of microhabitats occupied by *S. brunneus*.

Present Addresses:
[1]192 Castle Hill Ranch Road, Walnut Creek, CA 94595
[2]2380 Tuttle Circle, Reno, NV 89509

One, "Squirrel Manor," has relatively deep soils that facilitate drainage, whereas at the other two sites basalt lava bedrock lies close to the surface.

"Squirrel Manor"

This 1 ha site was located on a south-facing 5% slope 2 km S of Bear, Adams Co., Idaho (T19N, R3W, NW 1/4 Sec. 11) at 1325 m elevation in a relatively flat valley between Bear Creek and Steve's Creek. Nearby hillsides were forested with ponderosa pine (*Pinus ponderosa*) and other conifers. The 1 ha study plot was dominated by diverse bunch grasses (6-8 spp.) and forbs (25-30 spp.), with small clumps of big sagebrush (*Artemisia tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and Wyeth buckwheat (*Eriogonum heracleoides*). The reddish, clay-loam soil had few rocks and a depth in excess of 2 m.

"Riley Ranch"

The 4 ha study area (T19N, R3W, Sec. 34) was 8 km S of Squirrel Manor near Paradise Flat at 1370 m elevation on a 10% east-facing slope in a xeric meadow surrounded by ponderosa pine forest. The soil was a reddish skeletal loam with many basalt rocks at the surface weighing in excess of 100 kg. Soil depth varied from 30-70 cm at the center of the area to >1 m at the forest edges. The dominant plant was stiff sage (*Artemisia rigida*), with small amounts of bunch grasses, and spring forbs such as onions (*Allium* spp.), *Lomatium* spp., *Erigeron pumilus,* and camas (*Camassia quamash*) and 45% bare ground. Serviceberry (*Amelanchier alnifolia*), bitterbrush (*Purshia tridentata*), big sagebrush, rabbitbrush, and snowberry (*Symphoricarpos* spp.) occurred in deeper soils at the edges of the area. Columbian ground squirrels occupied the deep soils along the creek bottom at the east edge of the study site.

"Huckleberry"

This 2 ha site (T20N, R2W, Sec. 7) was located 10 km NNE of Squirrel Manor at 1490 m elevation in a meadow surrounded by ponderosa pine, Douglas fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) forests. The meadow was on an 8% south-facing slope with several low, rocky ridges and intervening grassy swales.

Our 2 ha study plot included two ridges and the swale between them. The ridges were dominated by *Eriogonum* spp., onions, *Lomatium* spp., *Gilia aggregata, Sedum stenopetalum,* and *Penstemon deustis* with 40% bare ground. The reddish, skeletal, sandy loam was 0-80 cm deep over basalt bedrock. The intervening swale was dominated by dense stands of grasses and forbs with 3% bare ground. The soil was a dark loam to sandy loam 1-2 m deep with few rocks.

Methods

Idaho ground squirrels were active above ground from late March until early August at the three sites. Burrows were excavated in late July and early August 1989 after the adults had immerged below ground into seasonal torpor and only a few young of the year remained active above ground. Attempts to trap squirrels at burrow entrances were unsuccessful, although at Squirrel Manor we had previously trapped squirrels at many of the burrow entrances excavated. In most cases, burrows could not be associated with squirrels of known age or sex.

At all three sites, we systematically excavated all burrow openings in a contiguous area (Squirrel Manor, 600 m^2; Huckleberry, 1500 m^2; Riley Ranch, 600 m^2) then excavated a few burrows of interest outside the selected area. At each burrow, the area around an arbitrarily chosen entrance was gridded into m^2 sections. Burrow entrance traps (Wobeser and Leighton 1979) were set at all entrances we could find within a 5 m radius.

Burrows were injected with expanding polyurethane foam (Felthauser and McInroy 1983) initially, but the method was abandoned because the foam cemented the rocks together making it difficult to remove the foam casting from the soil. We found it faster and more efficient to follow the burrows using hand tools.

Burrow systems were mapped on graph paper with depth measurements every 10 cm, or as necessary. Surface topography was determined using a transit. Lengths of the burrow systems reported below are horizontal distances rather than the running lengths of the tunnels, and depths are from the surface to the bottom of the chamber or tunnel.

Idaho ground squirrel burrow entrances were distinguished from those of other rodents at the sites (*Peromyscus maniculatus, Microtus montanus, M. longicaudus, Thomomys talpoides, Zapus princeps,* and *S. columbianus*) by size, direct observation of Idaho ground squirrel use, presence of

Idaho ground squirrel feces, recent wear at the burrow opening, and absence of soil mounds, Ambiguous burrows were omitted from the analysis. Idaho ground squirrels may modify burrows constructed by other species (see below). Hence, we focus here on burrow use, rather than burrow construction, by Idaho ground squirrels.

At each site, soil texture was determined using a hydrometer. Soil moisture was measured using a Bouyoucos soil moisture meter with soil moisture blocks buried at 30-60 cm. Soil temperatures were taken using a YSI telethermometer and thermister probes buried at 30-60 cm. Plant cover data were obtained using point frames. Soil texture, moisture, temperature, and plant cover data were collected as part of a separate study and will be reported in detail elsewhere.

Results

Although Davis (1939) reported that burrow openings were located under rocks and logs, we found 62 percent of the burrow openings in the open, 24 percent under rocks, and 14 percent under shrubs (see below). No logs were present at our three sites, although we did observe some burrow entrances under logs at other sites.

Idaho ground squirrel burrow openings were 4-15 cm wide ($\bar{x}$ = 6.3 ± 1.99 [SD]) and 4-17 cm high ($\bar{x}$ = 5.4 ± 2.04) and entered the ground at angles of 0° (into a slope) to 90° ($\bar{x}$ = 38.9° ± 22.1°). Tunnels were nearly round in cross section and 5-8 ($\bar{x}$ = 6.1) cm in diameter. Idaho ground squirrels rarely make soil mounds outside their burrow entrances; observations of captive squirrels and field observations of fresh burrows indicate that soil is scattered as it is brought to the surface.

We found two distinct categories of burrow systems: shallow (<50 cm maximum depth), simple systems lacking nests (hereafter, "auxiliary burrows"), and deeper (>50 cm maximum depth), more complex burrow systems with nests (hereafter, "nest burrows").

Nest burrows were longer (700-2600 cm) than auxiliary burrows (20-600 cm), deeper 50-121 cm (vs. 10-45 cm), with more entrances (3-11, $\bar{x}$ = 6.1 vs. 1-8, $\bar{x}$ = 1.8), more branch tunnels (2-13 vs. 0-4), and more chambers (1-7 vs. 0-2) (Table 1, all differences $p < 0.001$, Mann-Whitney U-tests).

TABLE 1. Idaho ground squirrel burrow characteristics at three study sites in Adams Co., Idaho. Values are means with range in parentheses.

site	n	max. depth (cm)	total length (cm)	# entrances
auxiliary burrows				
Squirrel Manor	19	24.6 (15-45)	147 (20-560)	1.8 (1-8)
Huckleberry	25	18.7 (0-30)	92 (20-500)	2.0 (1-3)
Riley Ranch	49	17.5 (0-40)	83 (15-600)	1.8 (1-6)
nest burrows				
Squirrel Manor	5	68 (53-80)	1092 (700-1320)	4.6 (3-7)
Riley Ranch*	2	86 (50-121)	2010 (1450-2600)	10.0 (9-11)

*One tunnel could not be followed below a large rock at 121 cm.

Auxiliary Burrows

We classified auxiliary burrows into four groups:

1) Horizontal burrows (Figure 1A). We examined 40 of these burrows that were superficially similar to shallow pocket gopher burrows. They were 25-600 ($\bar{x}$ = 147 ± 133) cm long, 10-44 ($\bar{x}$ = 19.0 ± 7.3) cm deep, and had 1-8 entrances ($\bar{x}$ = 2.1 ± 1.6). Most (30) were unbranched. In several cases, earth castings or sudden changes in tunnel diameter indicated that these were originally constructed by pocket gophers or voles and enlarged by ground squirrels.

2) Shrub-covered burrows (Figure 1B). These consisted of horizontal tunnels, or trenches roofed by branches of the shrub, that generally curved around the main root of the shrub and incorporated shrub canopy shape into the burrow design. The burrows were 15-280 ($\bar{x}$ = 69 ± 71) cm long and 10-30 ($\bar{x}$ = 16 ± 7.5) cm deep. There were 1-4 entrances ($\bar{x}$ = 1.9), often under the prostrate stems or canopy of the shrub. Some burrow systems were coextensive with one or more paths through the shrub. The shrub species used varied with the available species at each site: *Artemisia rigida* at Riley Ranch, *A. tridentata* and *Eriogonum heracleoides* at Squirrel Manor, and semishrubs of *E. sphaerocephalum* and *E. umbellatum* at Huckleberry. We found more shrub-covered burrows at Riley Ranch where shrubs were more abundant.

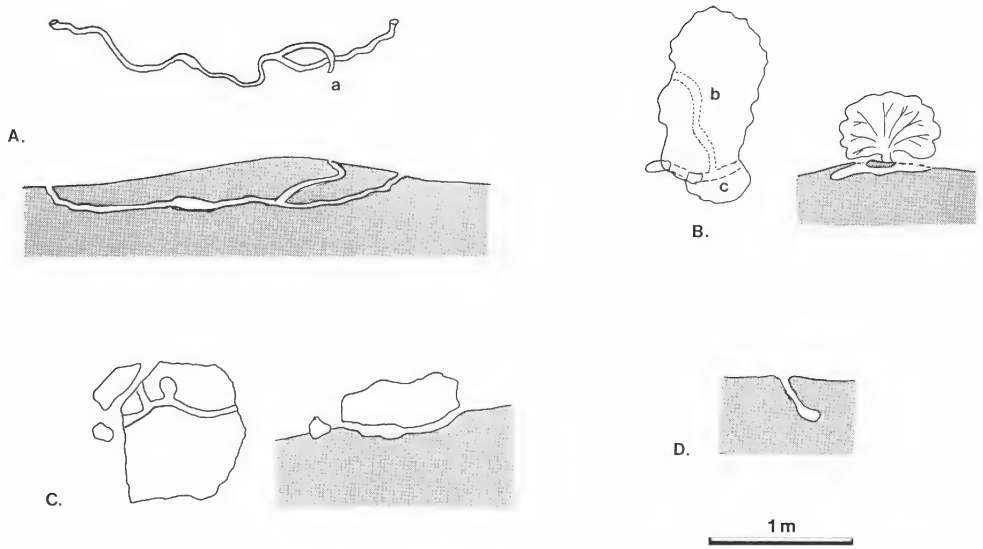

Figure 1. Auxiliary burrows of *Spermophilus brunneus*. A. Horizontal burrow, top view above, side view below; "a" indicates location of hidden entrance. B. Shrub-covered burrow, top view on left, side view on right; "b" indicates path beneath shrub; "c" indicates trench. C. Rock-covered burrow, top view on left, side view on right. D. Plunging burrow, side view. Ground is shaded.

3) Rock-covered burrows (Figure 1C). Tunnels were dug under large rocks (mostly 50 x 75 cm and larger) that were somewhat flat on the bottom and usually projected less than 15 cm below the surface. The burrows had 1-4 entrances ($\bar{x}$ = 1.9) opening at the lower edge of the rock, and were roofed by the rock itself, but sometimes continued into the soil upslope from the rock. The burrows were 15-160 ($\bar{x}$ = 64 ± 38.5) cm long. The tunnels usually converged below the rock, and frequently there was a small chamber at or near the point of convergence. These were found on the rocky hillsides at Huckleberry and Riley Ranch.

4) Plunging burrows (Figure 1D). These were short (20-120, $\bar{x}$ = 51 ± 28.6 cm), usually unbranched tunnels with a single entrance that entered the ground at a 15-90° ($\bar{x}$ = 40°) angle, continued down steeply to 11-45 ($\bar{x}$ = 23 ± 10.5) cm, and often ended in a small chamber. These occurred in open places away from rocks and shrubs, and were found at Huckleberry and Squirrel Manor.

Nests Burrows

We excavated seven nest burrows; all were located in deeper soils near ridge tops. Six of the nest burrows had a cluster of well-established entrances leading into a small, vegetated mound that was 10-20 cm tall and 1-3 m in diameter. The nest burrows built in mounds all had old, soil-filled tunnels that varied in distinctiveness and contained occasional remnants of old chambers. Thus the mounds were probably created by soil excavated by the squirrels over a period of many years. The nest burrow that lacked a mound was less complex and had no old, plugged tunnels.

Nest burrows had 3-11 entrances ($\bar{x}$ = 6.1 ± 3.1). Typically, at least one shallow tunnel extending for >1 m at <30 cm depth led into the burrow system (Figure 2). Tunnels leading to nests frequently dropped vertically 8-20 cm at some point (Figure 2) and rapidly descended to 45-50 cm depths. The nest chamber was at or near the lowest point in the burrow system, and was often near tunnel intersections.

Nest chambers were found at depths of 32-113 cm ($\bar{x}$ = 60.7 cm). Chambers were oval ($\bar{x}$ = 19 x 20 x 15 cm), but several had small pockets or other irregularities. The chambers were partially filled with nest material composed mostly of grasses, particularly *Bromus commutatus*, *B. tectorum*, *Poa bulbosa*, and *P. scabrella*. Leaves of

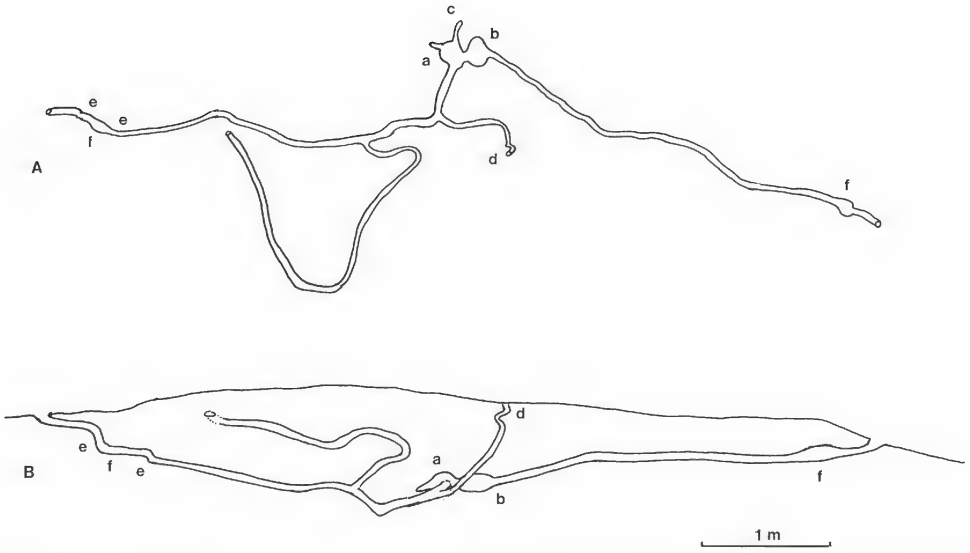

Figure 2. Nest burrow of *Spermophilus brunneus*. A. Top view, B. side view. Symbols: "a" old nest, "b" fresh nest, "c" feces-filled tunnel, "d" hidden entrance, "e" vertical drops, "f" chambers.

Lomatium nudicaule were abundant, but leaves of other dicots (*Eriogonum heracleoides* and *Amelanchier alnifolia*) were rare. Nests also included *Artemisia tridentata* bark, *Tragopogon dubius* and *Balsamorhiza* sp. seed heads, ponderosa pine needles, horse hairs, and feathers of a Brewer's Blackbird (*Euphagus cyanocephalus*). One nest was constructed almost entirely of mosses. Drains such as those described by Shaw (1926) and Edge (1934) were not found under the nests.

Nest burrows were inhabited by adults and larvae of darkling beetles (Tenebrionidae: *Eleodes* sp.) and crickets (Gryllidae). Fleas and mites were found in several nests.

Four burrow systems had a single nest, two systems had one old and one fresh nest, and one system had two fresh nests. The latter consisted of a deeper, more complex system connected with a simpler, shallower system via a plugged tunnel.

Additional Burrow Features

Hidden entrances (n = 18) were found in nest burrows and in shrub-covered and horizontal auxiliary burrows. These consisted of a nearly vertical, sometimes spiralling, tunnel that ended in an unusually small (4 cm diameter) entrance covered with leaf litter. Most hidden entrances were found below shrubs.

Vertical shafts found in four nest burrows and in one horizontal auxiliary burrow ascended from near the lowest portion of the burrow system and ended 3-4 cm below the surface. These resembled the vertical tunnels used by some Eurasian ground squirrels (*S. erythrogenys, S. fulvus, S. major, S. pygmaeus, S. suslica, S. undulatus*, and *S. xanthroprymnus;* Ognev 1947).

Short side tunnels measuring 5-10 cm long were found in both nest and auxiliary burrows. Penuska and Wade (1956) termed similar structures in Eastern chipmunk (*Tamias striatus*) burrows "galleries," and suggested they were probably used for turning around. We found galleries near entrances but occasionally elsewhere in both auxiliary and nest burrows.

Chambers were either widened areas of tunnels or hollows on the side of a tunnel that were much larger than galleries. They were largest in nest burrows ($\bar{x}$ = 9.2 x 9.8 x 10 cm, n = 9). The chambers in horizontal auxiliary burrows were about as wide and long as nest chambers, but not as tall ($\bar{x}$ = 6.0 cm, n = 10). The chambers at the end of plunging auxiliary burrows were slightly smaller ($\bar{x}$ = 8.2 x 9.7 x 6 cm, n = 10).

Chambers were found 30-300 cm ($\bar{x}$ = 152 cm) from the nearest entrance in nest burrows and we did not discern any pattern in their placement. Chambers were either empty or were filled with nest material, except for one with a food cache in the most complex burrow system excavated. The cache was in a chamber (25 x 20 x 12 cm) at 42 cm depth and contained 31 corms (35.4 g total) of bicolor biscuit-root (*Lomatium leptocarpum*).

Latrine chambers were not found, although feces were common in the deepest tunnels of a nest burrow, in two side tunnels near nests, and in rock-covered auxiliary burrows. Occasionally we found old, plugged tunnels that were full of feces in nest burrows.

Intersite variation

Frequencies of auxiliary burrow types differed significantly among sites ($p < 0.001$, G-test of independence using Williams' correction). The increase in rock-covered auxiliary burrows from Squirrel Manor (0) to Huckleberry (n = 10; 20%) to Riley Ranch (n = 14; 56%) paralleled the number of large rocks present at each site. There were also more shrub-covered burrows at Riley Ranch (n = 7; 28%) than at Squirrel Manor (n = 2; 11%) or Huckleberry (n = 5; 10%), and this also paralleled shrub abundance. The number of plunging burrows was highest at Huckleberry (n = 11; 22%) where there was more open ground. Horizontal burrows were more common and longer at Squirrel Manor (n = 13; 68%) and Huckleberry (n = 23; 47%) than at Riley Ranch (n = 4; 16%) where the soil was rockier. Squirrel Manor, which had the deepest auxiliary burrows, also had the deepest soils.

Burrow Locations

All nest burrows were located in well-drained soils >1 m deep. Four were near the top of a small ridge, and three were near the tops of slopes in deeper soil.

The proportion of Idaho ground squirrel habitat with deep soils apparently suitable for nest burrows was 3500 m^2 (35% of 1 ha) at Squirrel Manor, 1300 m^2 (7% of 2 ha) at Huckleberry, and 1950 m^2 (5% of 4 ha) at Riley Ranch.

Auxiliary burrows were located in both deep and shallow soils at all three sites, and in xeric and mesic plant associations, but marshy areas and seeps were avoided. Some auxiliary burrows occurred >100 m from the nearest known nest burrow.

At our study sites, we estimated that >90 percent of Idaho ground squirrel burrows were auxiliary burrows. Auxiliary burrows occurred at densities of 80-100/ha in the contiguous areas we selected for excavation.

Discussion

Townsend's ground squirrels also have two types of burrow systems which correspond to our nest and auxiliary burrows (Alcorn 1940, Reynolds and Wakkinen 1987, Reynolds and Laundre 1988). In these studies, auxiliary burrows were much more common than nest burrows. Because the function of auxiliary burrows is not established, we have preferred the neutral term "auxiliary" to such terms as "escape burrows," or "foraging burrows."

We found a squirrel in only one nest burrow. The animal was non-torpid and escaped. If the population was entering seasonal torpor and nest burrows are used as hibernacula, animals should have been in their nest burrows. Some sciurids (e.g., Shaw 1926, Holekamp and Sherman 1989, Kawamichi 1989) hibernate in special hibernation dens. We suspect that Idaho ground squirrels construct or separate burrows for hibernation, and that these have well-plugged entrances that we did not find despite careful searching. As evidence of this, at Huckleberry we found one burrow (not reported above) on 28 July 1989 with fresh soil around both entrances, indicating current construction. This burrow had 90 cm of horizontal tunnels and a steep descent to a small chamber at 45 cm. This may have been a hibernation den under construction by a juvenile, the only age class active at the time. P. W. Sherman (pers. comm.) has observed marked Idaho ground squirrels emerge from hibernation, use that burrow system for a few days, then move to the burrow system in which young are raised. These burrows have a single, steeply descending tunnel.

Variation in the proportions and dimensions of auxiliary burrow types between study sites in response to site characteristics seems reasonable. Grinnell and Dixon (1918) found that *S. beecheyi* made deeper burrows in softer soils. The ease of tunnel construction and availability of rocks and shrubs should influence the assortment of auxiliary burrows at a site.

All burrow entrances on rocky hillsides with shallow, seasonally water-logged soils led to auxiliary burrows. The squirrels did not nest there. However, we have observed *S. brunneus* using

these auxiliary burrows as temporary refuges, even when the soil was saturated. P. W. Sherman (pers. comm.) has seen *S. brunneus* emerge from burrow entrances with muddy fur.

Shaw (1924) concluded that drainage was important in Columbian ground squirrel nest burrow placement. Elliott (1983) found that Columbian ground squirrels placed 80% of their burrows in dry soil, 20 percent in moist soil, and 0% in wet soil, and all of the "permanent" (=nest) burrows were in the dry cover type. However, Weddell (1989) found that slope, position on slope, and number of native forbs were the most important variables for determining occupation of an area by Columbian ground squirrels. Columbian ground squirrel settlement in an area was also associated with the presence of other squirrels and burrows. Columbian ground squirrels were not restricted by soil texture, depth, or drainage, and she found burrows on shallow soils (25-51 cm to bedrock). However, Weddell did not indicate whether these were nest or auxiliary burrows.

Although the role of soil depth and moisture in determining nest site suitability for Idaho ground squirrels is not settled, we found no burrows we suspected of being nest burrows in soils <1 m deep. At most sites where *S. brunneus* occurs, there was a small area with deeper, well-drained soils not occupied by Columbian ground squirrels and usually an adjacent larger area with shallow, rocky soils (E. Yensen, pers. observations).

Areas with shallow soils are apparently used for foraging rather than nesting. Our frequent observations of Idaho ground squirrels foraging in those areas, the presence of numerous burrow openings, and the infrequent observation of Idaho ground squirrels in areas with deeper soils led to our mistaken impression that Idaho ground squirrels must somehow be able to nest in shallow soils. Abundant auxiliary burrows would allow protection for squirrels foraging on shallow soil at some distance from a nest burrow.

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The Effect of Observation Time and Sampling Frequency on Mean Daily Maximum, Minimum and Average Temperature

Abstract

The use of long-term temperature data for climatic, ecohydrologic and other studies must be scrutinized carefully because of the average daily differences due to time of observation (TOB). In this study, data from three climatic stations in the Reynolds Creek Watershed in southwest Idaho were used to determine if TOB had the same effect on average daily temperature at each location and if average temperature computed from 144 observations per day was the same as average temperature computed using the traditional method. No consistent differences between sites were found; however, in the spring and fall, average daily temperatures differed by as much as 1°C between 0600 and 1600 TOB. Average temperatures from 0700 and 0800 TOB were closest to midnight observations. Average temperatures from afternoon TOB were all higher than from midnight observations. Average daily temperatures computed from 10 min interval data, ending at TOB, were as much as 0.8°C less than the average computed from daily maximum and minimum values for 0800 through 1900 TOB. For 0600 and 0700 TOB, average temperatures computed from 10 min interval data were both less than and greater than averages computed by the usual method depending on time of year. The significance of our findings is that studies which require historical temperature records and where only small changes in temperature are expected, such as climate change modeling, will be difficult to verify. Also, mean daily temperature will change at locations when several readings are used to compute mean daily temperature rather than computing mean daily temperature from the daily maximum and minimum temperatures.

Introduction

It is often necessary to know maximum, minimum and mean daily temperatures for hydrologic, natural resource, and agricultural planning and development projects. This information is used to estimate rates and amounts of snowmelt, runoff, vegetation yields, and other temperature-related watershed processes through the use of ecohydrologic models such as SPUR (Simulation of Production and Utilization of Rangelands) (Wight and Skiles 1987) and ERHYM (Ekalaka Rangeland Hydrology and Yield Model) (Wight 1987). These models use either historic or synthetically generated daily climatic data as abiotic driving variables.

Historic maximum and minimum temperature records are also used for studies such as determining how emission of CO_2 and other gases affects climate. Based on present estimates, Abrahamson (1989) suggests that at the present rate, emission of gases will raise global temperature by at least 2°C by the year 2030.

Historic maximum and minimum temperatures used for modeling or for computing parameters in climate generation subroutines come from a few first order National Weather Service stations or from numerous cooperative observers who record the maximum and minimum temperatures daily. First order stations' maximum and minimum temperatures are recorded on a midnight to midnight basis, while the cooperative observers record temperature either in the morning or afternoon and the maximum and minimum values represent the 24-hour period ending at times of observation (TOB).

Several investigators, the first of whom was Ellis (1890), showed that in England mean monthly maximum, minimum, and mean temperatures were not the same depending on the ending time of the 24-hour observation period. He found that the mean maximum and minimum temperatures were generally warmer when the 24-hour observation period ended at 9:00 a.m. rather than at midnight. Donnel (1912), Rumbaugh (1934), Baker (1975), and Schaal and Dale (1977) found that mean daily temperatures (average of the daily maximum and minimum temperatures) were higher when the 24-hour period ended in the afternoon than when the period was midnight to midnight. They also found just the opposite effect when the 24-hour period ended at 8:00 a.m. The study by Schaal and Dale (1977) in Indiana showed that daily mean temperature for March was 0.7°C higher for the daily period ending at 7:00 p.m. than at midnight and 0.7°C cooler than midnight observations when the 24-hour period ended at 7:00 a.m. This variation in mean temperature values represents 70 percent of the 2°C temperature rise projected by

the year 2030 due to the greenhouse effect (Abrahamson 1989). These mean temperature differences from midnight TOB are because daily maximum temperatures generally occur in the afternoon and thus daily maximum readings occasionally represent the maximum temperatures on successive days with afternoon TOB. The opposite occurs for successive minimum temperatures when the TOB is in the morning. Edwards (1987) discusses errors due to undersampling and Karl *et al.* (1989) provides a lengthy discussion of errors that are due to type of instrumentation and location of instruments, etc. There is a need for accurate climatic data for eco-hydrologic modeling and for other investigations, such as assessment of climatic change.

The purpose of this study was: 1) to investigate the effect of TOB on maximum, minimum, and daily average temperature at three different elevations on a mountainous watershed; and 2) because of the availability of electronic recording equipment, to determine how well daily mean temperature which was calculated from hourly temperature values agree with the mean calculated from the average of the daily maximum and minimum, which is the common method of obtaining average daily temperature.

Study Area and Instrumentation

Temperature data from three locations on Reynolds Creek Watershed in southwest Idaho were used in this study. The watershed is a foothills tributary to the Snake River and is located approximately 64 km southwest of Boise, Idaho (Robins *et al.* 1965). As shown in Table 1, site elevation ranges from 1193 to 1895 m and thus represent different climatic regimes. Mean annual temperature ranges from 8.4°C at site A to 6.6°C at site C. Mean annual precipitation ranges from 233 mm at site A to 508 mm at site C for 1985-88.

At each of the sites, average hourly temperature and maximum and minimum temperatures during the hour were recorded electronically at the end of each hour. Average temperature during the hour was based on readings at 10 minute intervals during the hour. The maximum and minimum temperatures for 24-hour periods were obtained from the instantaneous 10-minute readings during the 24-hour period. Average temperatures were

TABLE 1. Average temperature, precipitation, and number of days of data for the three weather sites on Reynolds Creek Watershed, Idaho.

Site	Months						Annual Average
	Jan-Feb	Mar-Apr	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	
A (Elev. 1193 m)							
Average temperature (°C)	−0.84	6.01	14.57	20.16	11.36	−0.90	8.39
Average precipitation (mm) (1985-1988)	50	40	56	8	22	57	233
Average precipitation (mm) (1962-1988)	55	48	55	24	33	65	280
Number of days of temperature data	390	395	425	425	407	418	
B (Elev. 1649 m)							
Average temperature (°C)	−1.02	5.26	14.06	19.84	12.13	−0.63	8.27
Average precipitation (mm) (1985-1988)	64	60	65	13	25	65	292
Average precipitation (mm) (1962-1988)	67	66	71	27	40	78	349
Number of days of temperature data	203	228	243	248	235	243	
C (Elev. 1895 m)							
Average temperature (°C)	−1.79	3.20	11.70	17.81	10.19	−1.60	6.59
Average precipitation (mm) (1985-1988)	137	101	74	18	31	147	508
Number of days of temperature data	207	244	223	236	242	234	

computed from the maximum and minimum temperatures during the 24-hour period ending at TOB. The only temperature data used in this study were from days when all data were available during a seven-year period at site A and four-year periods at the other two sites. Temperature sensors were located in pagoda-style self-aspirating radiation shields at sites B and C and in a fan-aspirated shield at site A.

Results and Discussion

Time of Observation

The numerous different TOB used in the United States are evident from the information for Idaho which is listed in Table 2. The data in Table 2 were taken from the December 1987 climatological report (U.S. Department of Commerce 1987). Only six of the 138 climatological stations recorded maximum and minimum temperatures for the 24-hour period ending at midnight. Sixty-two stations' times of observations were during the morning between 0600 and 1000 with 46 stations having an 0800 observation time.

Sixty-nine stations had afternoon TOB between 1300 and 2100. One-half of the stations with afternoon TOB were at 1700 with most of the other observations at either 1600 or 1800. One station's TOB was at sunset.

There are at least two other TOB problems that affect Idaho data and data from other states. Idaho is divided into two time zones, Mountain and Pacific, so stations due north and south of each other with the same TOB are observed an hour apart. Also, Idaho observes daylight savings time which changes TOB of some locations, while other observers do not change the actual TOB. As discussed in the previous section, most times of observation in Idaho are on the hour either from 0600 through 0900 in the morning or 1600 through 1900 in the afternoon. Therefore, results from those hours are used in Table 3 and subsequent tables and discussions.

Average Daily Temperature Deviations

Deviations of average dailiy temperature from midnight observations from the Reynolds Creek Watershed sites are listed in Table 3. Deviations for 0600 are almost all negative and vary from close to zero for May and June to −0.4°C during the fall (September-October). The negative deviations change to almost all positive deviations by the 0900 TOB. The largest deviations for 0900 observations were in May and June when the deviation was about .3°C, while the smallest deviations were during the winter. Average morning TOB temperature deviations varied from −.22°C at 0600 to 0.16 at 0900, which indicates that average temperatures for hydrological and ecological studies from these two TOB will vary 0.38°C. On an annual basis, the 0600 and 0700 TOB average daily temperatures are the closest to midnight observations.

All of the deviations between midnight and the 1600 and 1900 TOB were positive. Deviations ranged from about 0.1°C during the fall for 1900 observations to about 0.9°C during May and June for 1600 observations. Afternoon time of observation temperature deviations were highest during the summer and least during the winter. Considering times of afternoon observations for all months, 1600 observation temperature deviations were

TABLE 2. Time of observation at Idaho climatological stations during 1987.

	AM Stations											
Hour	0600	0700	0800	0900	1000							Total
Number of stations	1	9	46	5	1							62
	PM Stations											
Hour	1300	1400	1500	1600	1700	1800	1900	2000	2100	2400	SS[1]	
Number of stations	1	1	0	9	35	16	4	2	1	6	1	76
												138

[1]Sunset

TABLE 3. Average daily temperature deviations (°C) from observations at midnight and the observation hour in which they occurred. Averages were computed from the maximum plus the minimum temperature divided by 2 for the 24 hour period ending at the time of observation.

Site	A (1193 m)							B (1649 m)							C (1895 m)							Average of 3 Sites
Month	Jan-Feb	Mar-Apr	May-Jun	Jun-Aug	Sep-Oct	Nov-Dec	Avg.[1]	Jan-Feb	Mar-Apr	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	Avg.	Jan-Feb	Mar-Apr	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	Avg.	
Time of Observation																						
0600	−.18	−.33	.02	−.25	−.41	−.16	−.22	−.26	−.28	−.01	−.11	−.33	−.15	−.19	−.14	−.35	−.18	−.18	−.40	−.17	−.24	−.22
0700	−.17	−.08	.26	.11	−.28	.19	−.06	−.27	−.11	.21	.16	−.25	−.16	−.07	−.13	−.24	.12	.14	−.37	−.15	−.11	−.08
0800	−.14	.16	.29	.15	.09	−.13	.07	−.20	.13	.30	.20	.03	−.13	.05	−.09	.03	.26	.25	−.06	−.12	.05	.06
0900	.12	.23	.30	.15	.16	.13	.18	−.05	.23	.37	.20	.15	−.01	.15	.02	.22	.38	.29	10	−.05	.16	.16
1600	.64	.73	.87	.60	.58	.41	.64	.30	.77	.91	.65	.49	.27	.57	.52	.76	.95	.75	.45	.35	.63	.61
1700	.51	.60	.72	.45	.39	.28	.49	.25	.67	.81	.53	.34	.21	.47	.46	.65	.84	.65	.29	.27	.53	.50
1800	.42	.47	.59	.31	.23	.20	.37	.21	.54	.63	.37	.19	.14	.35	.39	.50	.65	.49	.16	.21	.40	.37
1900	.38	.38	.44	.21	.11	.12	.27	.18	.43	.49	26	.12	.10	.26	.35	.40	.49	.37	.09	.15	.31	.28

[1]None of the annual average deviations, by time of observation, between sites was significantly different at the 0.05 level of probability.

greatest (0.61°C) and temperature deviations from 1900 observations were the least (0.28°C).

Average temperature deviations from afternoon observations were greater than from morning observations, which indicates that for climatic studies it is preferable to use data from stations where temperature is observed in the morning. The largest temperature deviation difference, between 0600 and 1600 TOB, was 1.07°C for March and April, which is about half of the projected world temperature increase by the year 2030 (Abrahamson 1989).

Effect of Elevation on Average Daily Temperature Deviations

One of the objectives of this study was to determine if average temperature deviations were affected by location (elevation) on the watershed. Location is of interest because, in mountainous areas, climatological data from valley sites are often adjusted to represent other areas that are at higher elevations. As seen in Table 3, there were no significant average temperature deviation differences between sites for any of TOB's. Because the average daily temperature deviations were not significantly different among sites, only data from site B were used in the following discussion and in Tables 4 and 5.

Average Daily Maximum Temperature Deviations from Midnight Observations

Average daily maximum temperature deviations were all zero or negative for morning times of observation. For each bimonthly period, temperature

TABLE 4. Average daily maximum and minimum temperature deviations (°C) from observations at midnight and 24 hour period ending at the time of observation, site B.

	Maximum Daily Temperature							Minimum Daily Temperature						
Month	J-F	M-A	M-J	J-A	S-O	N-D	Avg.	J-F	M-A	M-J	J-A	S-O	N-D	Avg.
Time of Observation														
0600	−.22	−.11	−.06	−.01	−.09	−.06	−.09	−.30	−.45	.04	−.21	−.58	−.24	−.29
0700	−.22	−.11	−.06	−.01	−.09	−.08	−.09	−.31	−.11	.48	.32	−.41	−.25	−.05
0800	−.20	−.10	−.05	−.01	−.10	−.07	−.09	−.20	.36	.65	.40	.15	−.19	.19
0900	−.13	−.07	.00	.00	−.04	−.04	−.05	.03	.54	.75	.41	.35	.02	.35
. . . . .														
1600	.36	1.03	1.07	.95	.69	.28	.73	.25	.51	.76	.35	.29	.27	.41
1700	.26	.83	.89	.73	.40	.18	.55	.24	.50	.72	.33	.28	.24	.39
1800	.21	.60	.62	.43	.12	.11	.35	.20	.49	.63	.32	.26	.17	.35
1900	.21	.44	.41	.22	.01	.06	.23	.15	.43	.57	.30	.23	.14	.30

TABLE 5. Average daily temperature deviations (°C) based on the difference between the average of the maximum and minimum temperatures and the average of 144 observations during the 24 hour period ending at the time of observation, site B (1649 m).

Month	Jan-Feb	Mar-Apr	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	Average
Time of Observation							
0600	−.14	.26	.03	.10	.20	−.06	.07
0700	−.12	.10	−.18	−.16	.11	−.05	−.05
0800	−.19	−.14	−.26	−.20	−.17	−.09	−.17
0900	−.32	−.25	−.33	−.22	−.31	−.21	−.27
. . . . .							
1600	−.65	−.76	−.81	−.68	−.70	−.55	−.69
1700	−.60	−.65	−.69	−.55	−.57	−.49	−.59
1800	−.54	−.53	−.50	−.40	−.42	−.42	−.47
1900	−.51	−.41	−.35	−.29	−.37	−.39	−.39
2400	−.42	−.02	−.03	.00	−.10	−.18	−.13

deviations were about the same for 0600, 0700, and 0800 TOB; however, deviations during the winter were more negative than during the summer. Summer average maximum deviations were very small or zero for the four morning TOB. The 0900 TOB most nearly represented midnight observations of average daily maximum temperature.

Average daily maximum temperatures for the four afternoon times of observation were all higher than midnight observations. The 1600 temperature deviations were up to 1.07°C for May-June. The smallest deviations were from 1900 observations; however, they were as high as +0.44°C for March and April. These results show that morning observations of average daily maximum temperature represent midnight observations closer than afternoon TOB.

One of the problems of using temperature data for long-term climatic studies has been consistent TOB throughout the record (Schaal and Dale 1977). Data from this study indicate that changing TOB between 0600 and 1600 can change the average maximum temperature by 1.1°C during the period, March through June.

Average Daily Minimum Temperature Deviations from Midnight Observations

Morning, average daily minimum temperature deviations vary from mostly negative at 0600 to all positive at 0900. Average minimum temperatures varied almost 1°C between 0600 and 0900 times of observation during the spring and fall. These variations are about the same as observed for morning and afternoon variations for average daily maximum temperatures. On an annual basis, the 0700 TOB represented midnight observations more closely (−0.05°C) than any other TOB; however, during the year, deviations varied from 0.48°C for May and June to −0.41°C for September and October.

Afternoon average daily minimum temperature deviations were all positive and on an annual basis only varied between 0.30°C at 1900 to 0.41°C for 1600 TOB. Average minimum temperature deviations during May and June were highest (0.67°C) and lowest (0.21°C) during the November through February period.

Effect of Sampling Frequency on Average Daily Temperature

The information presented in Table 5 was obtained by subtracting the average temperature based on the maximum and minimum temperature during the 24 hr period ending at TOB from the average of 10 min observations (144 observations/day) during the same time period. These analyses were done to determine how average daily temperatures recorded electronically, the method used presently in most scientific studies, compare with average daily temperatures obtained by the more conventional method of averaging the daily maximum and minimum temperatures for a given TOB.

Most of the deviations for all TOB, except 0600 and 0700, were negative, therefore average daily temperature computed from 10 min data will be cooler than average daily temperatures computed from the average of the daily maximum and minimum temperature. This condition was most pronounced for afternoon TOB where, on an annual basis, the 10 min average temperature was 0.69°C cooler than that from maximum and minimum temperatures for the 1600 time of observation.

Average annual deviations were the least for 0600 and 0700 TOB observation when there were both positive and negative deviations. For 0600 TOB, deviations were negative during the winter and positive the remainder of the year, and were not more than .25°C for any bimonthly period. There were two bimonthly periods, March-April and September-October, at the 0700 TOB, when temperature deviations were positive and temperature deviations were negative for all other TOB.

For three of the bimonthly periods, March-August, inclusive, midnight observation temperature deviations were zero or nearly zero. Temperature deviation for the November-December period was −0.18°C which were temperature deviations in the same range as those for morning TOB. The average temperature deviation was −0.13°C which was one of the smallest values but a greater temperature deviation than that of 0600 and 0700 TOB.

There are two reasons why average daily temperatures computed from 10 min records are less than the average computed from daily maximum and minimum temperatures (Table 5). The first reason is that, in general, the number of hours during a day with warm temperatures is less than the number of hours with cool temperatures in the environment on Reynolds Creek Watershed. Secondly, the higher average daily temperatures computed from daily maximum, and minimum temperatures are more pronounced for afternoon times of

observation. This is because maximum readings often fall on or about the time of observation and thus maximum values for successive days were obtained from the same afternoon and could have been the same temperature if the maximum temperature occurred at the TOB.

The average daily temperature computed from 10 min observations was higher than the average based on daily maximum and minimum temperatures for most of the 0600 TOB, and the 0700 TOB during the spring and fall (Table 5). This is because 0600 and 0700 hours are at the time of minimum daily temperature and thus minimum values for successive days actually were obtained from the same morning. This winter minimum temperature effect was greater than that from more hours of minimum temperatures during most days as discussed above.

Conclusions

Analyses of temperature data from three climatic stations in the Reynolds Creek Watershed in southwestern Idaho show the following:

1. Average daily temperature during the March-April period differed by as much as 1°C between 0600 and 1600 TOB when average temperature was computed as the average of the maximum and minimum temperatures between observations.
2. On an annual basis, average daily temperatures from 0700 and 0800 observations were within 0.08°C of midnight observations; 0600 observations were 0.22°C less than midnight observations; and afternoon times of observation temperatures were greater than those computed from midnight observations by as much as 0.61°C for observations at 1600.
3. May-June temperature deviations of about 0.9°C for 1600 TOB were the greatest differences from midnight observations.
4. Average daily temperatures computed from 0800 TOB were the closest to midnight observations for most bimonthly periods and on an annual basis.
5. Average daily maximum temperature computed from morning TOB were within −.09°C of midnight observations but were as much as .22°C cooler for the months of January-February.
6. Average daily minimum temperature computed from afternoon TOB were all higher than from midnight observations and were as high as .76°C for the 1600 TOB during the May-August period. The average deviations varied from .21°C during January and February to .67°C for the May-June period.
7. In general, average daily temperatures computed from numerous observations during a 24-hr period were lower than the daily averages computed from the daily maximum and minimum temperatures. This difference is greatest for 1600 TOB and least for 0600 and 0700 TOB.

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Differential Vulnerability of Small Mammals and Amphibians to Two Trap Types and Two Trap Baits in Pacific Northwest Forests

Abstract

A variety of sampling techniques are available to sample small mammals and amphibians, but an assessment of the least biased method to sample species assemblages is necessary to adequately describe community structure. We compared capture rates of small mammals and amphibians between pitfall and Museum Special traps in six mature forest stands in the central Oregon Coast Range in the spring, 1988. Fewer small mammal and amphibian species were caught with Museum Special traps than with pitfalls. Townsend's chipmunks (*Tamias townsendii*) and deer mice (*Peromyscus maniculatus*) were more vulnerable to capture in Museum Specials than in pitfalls. Pacific giant salamanders (*Dicamptodon ensatus*) and western red-backed salamanders (*Plethodon vehiculum*) were captured exclusively in pitfalls. Shrew-moles (*Neurotrichus gibbsii*), Pacific water shrews (*Sorex benderii*), Trowbridge's shrews (*S. trowbridgii*), and Pacific shrews (*S. pacificus*) were more vulnerable to pitfall than Museum Special capture. Western red-backed salamanders, shrew-moles, Trowbridge's shrews, and western jumping mice (*Zapus trinotatus*) were more vulnerable to capture in pitfalls with water present than to capture in dry pitfalls. Townsend's chipmunks were more vulnerable to capture by Museum Specials baited with peanut butter than baited with meat paste. Pitfalls partially filled with water and Museum Specials baited with peanut butter were the most effective methods tested.

Introduction

There are many established methods for trapping small mammals and amphibians. Comparisons of captures among pitfalls, snap traps, and live traps suggest that no one technique is appropriate for all species, and that results vary geographically (Bury and Corn 1987, Block *et al.* 1988, Szaro *et al.* 1988, Taylor *et al.* 1988). Several studies indicated that amphibians and Soricid mammals are more vulnerable to capture in pitfall traps than in Museum Special snap traps (Brown 1967, Williams and Braun 1983, Bury and Corn 1987, Taylor *et al.* 1988). Bury and Corn (1987) and Taylor *et al.* (1988) suggested that pitfalls were superior to Museum Specials in capturing many small mammal and amphibian species in forests of western Oregon and Washington. Bury and Corn (1987) suggested that a combination of pitfalls and Museum Specials were necessary to fully sample small mammal communities in these forests. However, Bury and Corn (1987) and Taylor *et al.* (1988) specifically excluded riparian areas from their study sites, and their comparison of Museum Specials with pitfalls was not paired in time nor space within each forest stand. Williams and Braun (1983) compared pitfalls with Museum Specials in riparian and upland areas of northern California, but their study was not replicated and their number of trap nights (TN) with Museum Specials was small (n = 500).

Pitfalls have been used in a variety of ways to capture and sample small mammals and amphibians. Williams and Braun (1983) and Bury and Corn (1987) tested several pitfall array designs and concluded that pitfalls without drift fences were as effective at sampling mammals as pitfalls with drift fences when three times as many single pitfalls were used. These authors and Pankowoski (1979) used pitfalls as kill traps (through adding water or accumulation of precipitation), whereas others (Brown 1967, Boonstra and Krebs 1978) have used dry pitfalls as live traps. The degree to which water in pitfalls influences captures of small mammals and amphibians and the comparative effectiveness of Museum Specials and pitfalls without drift fences has, to our knowledge, not been investigated in a replicated, experimental design.

Museum Specials have been criticized as being less effective than pitfalls for trapping Soricids. However, West (1985) demonstrated that the new model of Museum Special (with plastic treadles) was more effective at capturing Soricids than the old model. Thus, we wished to determine if

pitfalls were more effective at capturing Soricids than the new Museum Special. Further, most previous investigators (e.g., Williams and Braun 1983, Taylor *et al.* 1988) used peanut butter and oats for bait. Soricids are carnivorous, so we compared the effectiveness of a bait made of meat paste with peanut butter.

Our null hypotheses were: 1) capture rates for small mammal and amphibian species would not differ between pitfalls and new Museum Specials; 2) capture rates for small mammal and amphibian species would not differ between pitfalls with water and pitfalls without water, and 3) capture rates for small mammal species would not differ between Museum Specials baited with peanut butter and Museum Specials baited with meat paste.

Methods

The study was located in the Drift Creek watershed, Lincoln County, Oregon (Figure 1). We sampled six unmanaged, mature forest stands which originated following extensive fires in the mid-1800's. Stands were characteristic of the western hemlock (*Tsuga heterophylla*) vegetation zone of the Oregon Coast Ranges (Franklin and Dyrness 1973). Overstory vegetation varied among sites but was dominated by Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*); other tree species included western hemlock, western redcedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*). Understory vegetation was patchily distributed and dominated by salmonberry (*Rubus spectabilis*), swordfern (*Polystichum munitum*), vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and huckleberries (*Vaccinium* spp.).

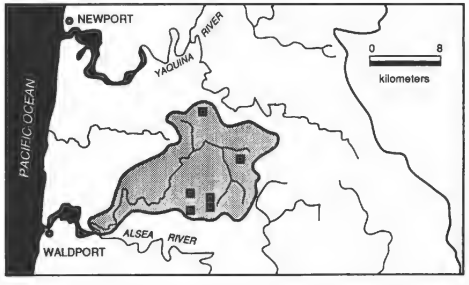

Figure 1. Location of study areas, Lincoln County, Oregon.

We established two 700-m transects in each stand: one along a second- or third-order stream and another 400 m upslope and parallel to the streamside transect. Two 400-m transriparian transects extended from the streamside transect to the upslope transect. We placed pitfall stations at 100-m intervals along the upslope and streamside transects and at 50-m intervals along the transriparian transects for a total of 30 stations per stand. At each station we subjectively located two pitfalls within 5 m of the station. Each pitfall was set level with the surface of the ground. Pitfalls were set adjacent to logs (63%), slope breaks (19%), in slash (11%) or adjacent to rocks (3%). Logs adjacent to pitfalls ranged from 1 to 20 m in length and were distributed among large (>49 cm, 46%), medium (20-49 cm, 32%), and small (<19 cm, 23%) diameters.

Pitfalls were made of two #10 tin cans (36 cm deep and 15 cm in diameter) held together with duct tape (Corn and Bury 1990). All pitfalls had 3-4 drainholes about 4 cm from the bottom to keep the traps from filling to the top with water which could allow animals to escape. Half of the pitfalls had a drain hole in the bottom to keep the trap free of water during sampling. One pitfall with a drain hole (dry pitfall) and one without a drain hole (wet pitfall) was set at each station. However, drain holes in the bottom of pitfalls were only marginally successful in keeping pitfalls dry. As a result, sampling intensity with wet pitfalls was consistently higher (1246-1704 TN/stand) among stands than dry pitfalls (96-554 TN/stand). Comparisons of community structure between the two types of pitfalls were not possible because of unequal sampling intensities. No bait was used in pitfalls.

We placed snap-trap stations at 20-m intervals along the upslope and riparian transects and at 10-m intervals along the transriparian transects for a total of 150 stations per stand. We subjectively located two Museum Special traps of the new design (with plastic treadles) within 2 m of each snap trap station. One Museum Special was baited with peanut butter and rolled oats and one was baited with meat paste and rolled oats. The meat paste consisted of a mixture of liverwurst and vegetable oil. Traps were set adjacent to or under some form of natural cover, typically along natural runways. Traps were set for 5 consecutive days in each stand and they were checked and rebaited daily.

We sampled stands between 24 April and 28 June 1988 in random order. Sampling was initiated in a new stand every seven days for a total of six

weeks. Within each stand, we set and checked Museum Specials daily during the first five sampling days; the pitfalls were opened and checked weekly for 30 consecutive days. As a result of staggered sampling periods, Museum Special sampling was completed on 2 June (9,000 TN), while pitfall sampling was not completed until 28 June (10,800 TN). Precipitation data collected at Tidewater, OR, within 4-12 km of the study sites indicated that, over the 30-day sampling period in each stand, there was an average of 15 days with measurable rain per stand per 30 days (range = 10-19). Precipitation per stand per 30 days averaged 21 cm (range = 8-27 cm).

We calculated captures per 1,000 TN for each species by trap type within each stand. For each species, we compared capture rates between trap types, pitfalls with and without water, and snap trap baits with a Wilcoxon sign-rank test. Each stand was considered an independent observation (n = 6) and only species with >20 captures were included in statistical analyses.

To assess if logs, slope breaks, and rocks act as natural drift fences, we compared lengths of these features at pitfalls that captured a species with those that did not capture that species with Student's *t*-test. To determine if pitfalls adjacent to logs were more effective than pitfalls adjacent to other features, we compared captures along logs vs. along other features with Pearson's chi-square using Yates correction for small samples.

Because investigators often use trap results to compare community structure between or among habitats, we compared estimates of Shannon-Weaver species diversity ($H' = -\ p_i \log p_i$), equitability ($E = H'_{observed}/H'_{max}$), and richness (number of species) (Brower and Zar 1984) between pitfalls and Museum Specials using a Wilcoxon sign-rank test. We also calculated percent community similarity (PS) between sampling methods on each site to illustrate any biases in estimates of community composition between techniques. Percent similarity was defined as the sum over species of the lowest percentage of contribution of each species to either community (Brower and Zar 1984).

Results and Discussion

Pitfalls vs. Museum Specials

Pitfalls were more effective than Museum Specials in sampling amphibians (Table 1). Only one tailed frog (*Ascaphus truei*) and six rough-skinned newts (*Taricha granulosa*) were captured in Museum Specials. In contrast, 245 individuals representing eight species of amphibians were captured in pitfalls (Table 1). Most in low numbers, probably because sampling extended into late June when surface activity is reduced by lack of precipitation.

For most species of small mammals that were effectively sampled in this study (>20 captures), pitfalls were more effective than Museum Specials. Total number of individuals captured and species richness were greater in pitfalls than in Museum Specials (Table 1). Pacific shrews, Pacific water shrews, Trowbridge's shrews, and shrew-moles were captured more frequently in pitfalls than in Museum Specials. Despite the increased propensity for the new style of Museum Special to capture Soricids (West 1985), pitfalls were still more effective in sampling this group than the new style of Museum Specials. One dusky-footed woodrat (*Neotoma fuscipes*) was captured in a Museum Special. Deer mice and Townsend's chipmunks were also captured most frequently in Museum Specials. Estimates of small mammal species equitability was higher in the Museum Special sample than in the pitfall sample (Table 1), largely because of the reduced number of Soricids, especially Trowbridge's shrews, in the Museum Special sample. Pitfalls and Museum Specials produced dissimilar estimates of small-mammal community structure (PS = 42%) due to sampling bias in the two trap types.

Pacific jumping mice were less likely to be caught in pitfalls set along logs (observed = 53, expected = 67) than along rocks, slash, slope breaks or in the open (chi-square = 7.28, df = 1, p = 0.010). California red-backed voles (*Clethrionomys californicus*) were caught in pitfalls adjacent to features that were longer (5.0 m, SE = 0.4, n = 79) than features at pitfalls that did not capture them (3.8 m, SE = 0.3, n = 174, p = 0.015). Hence, the use of pitfalls to compare relative abundances of jumping mice and California red-backed voles among stand types should be standardized with respect to placement of pitfalls adjacent to logs. Other species were captured as expected in relation to forest floor features adjacent to traps.

Pitfalls With and Without Water

Pitfalls with water were more effective than dry pitfalls in sampling amphibians. Although total

TABLE 1. Average captures per 1,000 trap nights (TN) in pitfalls (10,800 TN) and Museum Specials (9,000 TN), in six sub-basins of the Drift Creek Basin, Lincoln County, Oregon, April-June 1988 (standard errors in parentheses).

Species	Pitfall (n = 6)	Museum Special (n = 6)	p[1]
Amphibians			
Ascaphus truei	3.6(0.7)	0.1(0.1)	0.036
Dicamptodon ensatus	1.9(0.3)	0.0(0.0)	0.036
Plethodon vehiculum	3.4(1.4)	0.0(0.0)	0.036
Number of individuals[2]	22.3(3.9)	0.8(0.5)	0.036
Number of species	6.3(0.4)	0.7(0.3)	0.036
Mammals			
Clethrionomys californicus	11.7(2.5)	11.2(2.2)	0.834
Microtus oregoni	1.0(0.6)	1.5(0.6)	1.000
Neurotrichus gibbsii	3.9(0.7)	0.1(0.1)	0.036
Peromyscus maniculatus	2.4(1.4)	21.9(7.8)	0.036
Sorex benderii	8.8(1.1)	1.1(0.4)	0.036
Sorex pacificus	17.2(2.2)	4.1(0.9)	0.036
Sorex trowbridgii	85.6(7.3)	10.2(1.9)	0.036
Tamias townsendii	0.0(0.0)	6.2(1.1)	0.036
Zapus trinotatus	10.0(2.3)	3.1(1.0)	0.059
Number of individuals[3]	247.3(27.7)	90.7(12.7)	0.036
Number of species	11.3(0.3)	8.8(0.3)	0.036
Diversity (H')	0.60(0.03)	0.73(0.05)	0.093
Equitability	0.57(0.02)	0.82(0.03)	0.036
Community similarity (%)	41.7(5.3)		

[1]Wilcoxon Sign-Rank test.

[2]Includes species captured in pitfalls (P), Museum Specials (M) or both (B): *Aneides ferreus* (P), *Ensatina eschschlotzi* (P), *Plethodon dunni* (P), *Rana aurora* (P), *Rhyacotriton olympicus* (P), and *Taricha granulosa* (B).

[3]Includes species captured in pitfalls (P), Museum Specials (M) or both (B): *Aplodontia rufum* (P), *Microtus longicaudus* (B), *Mustela erminea* (P), *Neotoma fuscipes* (M), *Phenacomys albipes* (B), *Phenacomys longicaudus* (P), *Scapanus orianus* (P), *S. townsendii* (P), *Sorex vagrans* (P), and *Thomomys mazama* (P).

number of individuals captured was slightly higher in wet than in dry pitfalls, we were able to detect statistically significant differences in capture rates between dry and wet pitfalls only for western red-backed salamanders (Table 2). Water in pitfalls may attract some amphibians, especially in upslope areas. Therefore, we compared capture rates between wet and dry pitfalls for three amphibian species at stations >200 m from permanent water. Tailed frogs were captured exclusively in wet pitfalls (2.9/1000 TN, SE = 0.7, p = 0.0360) on these upland sites. Pacific giant salamanders (wet = 2.7/1000 TN, SE = 0.9; dry = 0.9, SE = 0.9) and western red-backed salamanders (wet = 3.8/1000 TN, SE = 2.2; dry = 0.8/1000 TN, SE = 0.8) were captured more frequently in wet pitfalls on upland sites, but these differences were not significant (p = 0.180 and 0.090, respectively).

Overall capture rates for small mammals were higher in wet than in dry pitfalls; this difference was significant for shrew-moles, Trowbridge's shrews, and Pacific jumping mice (Table 2). Shrew-moles were caught exclusively in pitfalls with water. Only Oregon voles (*Microtus oregoni*) were captured more frequently in dry than in wet pitfalls, yet even dry pitfalls captured as many or more Soricids and jumping mice per 1000 TN as Museum Specials.

Water in pitfalls likely reduces the chances of escape for small mammals capable of leaping out of dry pitfalls, which may explain why jumping mice were captured less often in dry pitfalls. Dry pitfalls seem to have the potential for capturing most small mammal species alive and could serve as an effective live-trapping method. Shrew-moles may be missed in dry pitfall sampling and more pitfalls may be needed to compensate for reduced capture rates of other species.

Peanut Butter vs. Meat Paste

Overall, Museum Specials baited with peanut butter captured more individual mammals than traps baited with meat paste, although Townsend's chipmunk was the only species captured significantly more with peanut butter (Table 3). No species

TABLE 2. Average captures per 1,000 trap nights (TN) in pitfalls with (8,451 TN) and without (2,349 TN) water, in six sub-basins of the Drift Creek Basin, Lincoln County, Oregon, April-June 1988 (SE in parentheses).

Species	Water (n = 6)	Dry (n = 6)	p[1]
Amphibians			
Ascaphus truei	4.1(0.8)	1.8(1.0)	0.096
Dicamptodon ensatus	2.1(0.7)	2.5(1.6)	0.402
Plethodon vehiculum	3.7(1.4)	1.5(1.0)	0.036
Number of individuals[2]	13.5(2.4)	6.7(1.6)	0.094
Mammals			
Clethrionomys californicus	13.3(3.0)	7.4(3.0)	0.208
Microtus oregoni	0.7(0.6)	2.3(1.3)	0.201
Neurotrichus gibbsii	4.5(0.7)	0.0(0.0)	0.036
Peromyscus maniculatus	3.0(1.7)	2.6(1.8)	0.855
Sorex benderii	8.5(1.7)	4.8(2.7)	0.529
Sorex pacificus	17.4(2.7)	10.0(2.5)	0.142
Sorex trowbridgii	93.7(7.5)	41.8(10.3)	0.036
Zapus trinotatus	11.9(2.7)	2.9(1.7)	0.036
Number of individuals[2]	158.3(12.9)	74.1(10.2)	0.036

[1]Wilcoxon Sign-Rank test.
[2]Includes species captured in pitfalls (W), dry pitfalls (D), or both (B): *Aneides ferreus* (B), *Ensatina eschschlotzi* (W), *Plethodon dunni* (B), *Rana aurora* (W), *Rhyacotriton olympicus* (B), and *Taricha granulosa* (B).
[3]Includes species captured in pitfalls with water (W), dry pitfalls (D), or both (B): *Aplodontia rufum* (B), *Microtus longicaudus* (W), *Mustela erminea* (W), *Phenacomys albipes* (W), *Phenacomys longicaudus* (W), *Scapanus orianus* (B), *S. townsendii* (W), *Sorex vagrans* (B), and *Thomomys mazama* (W).

TABLE 3. Average captures per 1,000 trap nights (TN) in Museum Specials using peanut butter (4,500 TN) and meat paste (4,500 TN) as baits, in six sub-basins of the Drift Creek Basin, Lincoln County, Oregon, April-June 1988. (SE in parentheses).

Species	Peanut Butter (n = 6)	Meat Paste (n = 6)	p[1]
Sorex benderii	0.7(0.5)	0.9(0.4)	0.893
Sorex pacificus	1.8(0.6)	2.9(0.6)	0.182
Sorex trowbridgii	5.1(0.9)	4.4(1.7)	0.529
Clethrionomys californicus	5.8(1.9)	3.3(0.9)	0.225
Microtus oregoni	1.8(1.1)	0.7(0.3)	0.273
Peromyscus maniculatus	15.1(5.7)	7.5(4.4)	0.059
Tamias townsendii	5.8(1.3)	1.8(0.6)	0.036
Zapus trinotatus	3.1(1.3)	1.6(0.6)	0.215
Number of individuals[2]	57.2(6.3)	33.5(6.9)	0.036
Number of species	7.3(0.4)	7.5(0.3)	0.855
Diversity (H')	0.69(0.04)	0.71(0.04)	0.529
Equitability	0.80(0.04)	0.82(0.04)	0.675
Community similarity (%)	75.6(3.4)		

[1]Wilcoxon Sign-Rank test.
[2]Includes species captured with peanut butter (P) or both baits (B): *Phenacomys albipes* (B), *Microtus longicaudus* (B), and *Neotoma fuscipes* (P).

preferred the meat paste. Estimates of community structure were quite similar (PS = 75.6%) (Table 3). Differences in captures of mammals did not seem to be a result of the meat paste simply being washed away sooner during rainy periods. The average difference in captures of mammals per day between bait types (paired *t*) did not differ significantly between days with rain during the previous 24 hours (5.4, SE = 1.1, n = 17) and days without rain during the previous 24 hours (3.9, SE = 0.9, n = 15, p = 0.28). Further, the difference in captures of mammals per day between bait types was not associated (Pearson correlation) with the amount of precipitation during the previous 24 hours (r = 0.19, p = 0.30).

Conclusions

Our evidence suggests that a combination of techniques that include pitfall and Museum Special sampling would be most effective to estimate presence and abundance of most small mammal and amphibian species in mature forest including riparian areas. In this study, pitfalls were successful in capturing more species and more individuals of most species than were Museum Specials. Museum Specials are needed only because pitfalls do not effectively sample deer mice and Townsend's chipmunks, two common species (Fig. 2). If only one type of trap is used, then pitfall sampling would be most effective, particularly for the less common species (e.g., some of the Soricids). Also, pitfalls with water were more effective in capturing most small mammal and amphibian species than dry pitfalls; pitfalls with water should be considered the trap of choice for sampling amphibians, Soricids, and jumping mice. But pitfall placement was much more labor intensive than snap-trap placement and maintenance.

If snap trapping is the chosen sampling method, then Museum Specials baited with peanut butter and oats would be simpler, cheaper, and generally more effective than traps baited with meat paste and oats. Furthermore, peanut butter would be the preferred bait for sampling Townsend's chipmunks. Given West's (1985) finding that the new design of Museum Special may be less likely to capture chipmunks than the old design, then the old design baited with peanut butter may be the best option for sampling this species.

Not surprisingly, no trap type or trap bait adequately sampled all terrestrial small mammal and amphibian species present in this study. We suspect, for example, that Olympic salamanders (*Rhyacotriton olympicus*) and red-tree voles (*Phenacomys longicaudus*) were likely more common than our estimates indicated. All sampling methods were biased for or against some species, consequently estimates of community structure vary depending on the combination of techniques used. Based on our results, the use of pitfalls with water and Museum Specials baited with peanut butter, in combination with time-constrained searches and aquatic searches for more cryptic forms (e.g., Olympic salamanders) may provide the least biased estimate of terrestrial small-mammal and amphibian community structure. The combination of pitfalls with water and Museum Specials with peanut butter effectively sampled a broader range of small mammals than either technique individually (Fig. 2). The technique chosen obviously influences estimates of community structure because of inherent biases in any one technique. Indices to community structure are not comparable among data sets unless data sets can be combined in an unbiased and objective manner. Further, habitat relationships derived from different sampling techniques may vary among techniques (Taylor *et al.* 1988), so use of the most effective capture technique for each species is recommended to reduce this bias.

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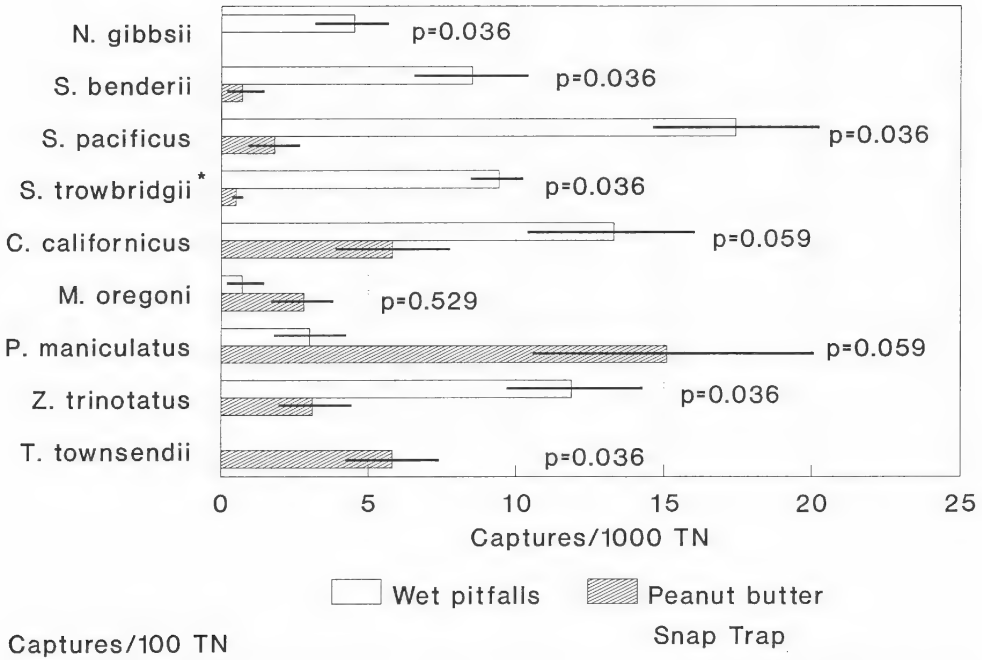

Figure 2. Captures/1000 trap nights of small mammals using pitfalls with water compared to Museum Specials baited with peanut butter in six sub-basins of the Drift Creek Basin, Lincoln County, Oregon, 1988. Standard errors indicated by bars. *S. trowbridgii* are in captures/100 trap nights. Probability values are associated with *a posteriori* comparisons using Wilcoxon Sign-Rank test.

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The Origin of *Lamium hybridum*, A Case Study in the Search for the Parents of Hybrid Species

Abstract

An unusual ("new") form of *Lamium* was observed growing sympatrically with *Lamium amplexicaule* L. and *L. purpureum* L. in northwestern Washington. The new taxon was noted to have characteristics more or less intermediate between these species, suggesting hybrid derivation. An observed lack of morphological segregation also suggested allopolyploidy. Taximetric (based on morphological and flavonoid variables), electrophoretic, and cytological analyses were carried out to test the hypotheses that the new taxon is a hybrid between *L. amplexicaule* and *L. purpureum*, that it is an amphidiploid (allopolyploid), and that hybridization occurred *in situ*. The experimental results confirm that the intermediate is a tetraploid and strongly implicate *L. purpureum* (2*n*) as a parental species. However, the results equally imply that *L. amplexicaule* (2*n*) is not the second parent; obviously, the new (hybrid?) species was not produced *in situ* but was introduced. A review of the literature and search of selected herbaria resulted in the identification of the new taxon as *Lamium hybridum* Vill., a European species. So, while the results of this study do not support the hypothesis of a new case of allopolyploidy, they exemplify the methodology used in tracing the parentage of hybrid species.

Introduction

I recall as a graduate student, while very much in the formative years of my profession, being told by my mentor, Marion Ownbey, that one of the primary responsibilities of systematists was to observe and document evolution at work. Certainly, Ownbey met that responsibility with his discovery and documentation of *Tragopogon mirus* and *T. miscellus*, amphidiploids (allopolyploid species) derived from hybridization of *Tragopogon dubius* X *T. porrifolius* and *T. dubius* X *T. pratensis* respectively (Ownbey 1955). Marion Ownbey was a first class plant systematist and a meticulous researcher; but he was also extremely lucky. Although we accept the premise that more than half of all angiosperm species were derived from hybridization followed by chromosome doubling (allopolyploidy), his are two of the few cases where this has actually been observed to occur naturally. So it was that in the spring of 1986 I became very excited upon discovering a small population of what appeared to be a new hybrid species. The new taxon was growing sympatrically with *Lamium amplexicaule* L. and *L. purpureum* L.; it was more or less intermediate between these two species; and, very importantly, there was very little variation among the plants, suggesting a stabilized F1 population rather than a hybrid swarm. Furthermore, the plants were more robust than the two known species, suggesting that they were polyploids-allopolyploids! Several questions came to mind: (1) Was this in fact a hybrid species? (2) Was it an allopolyploid? (3) If it were a hybrid, did hybridization occur *in situ* or was the plant introduced as a hybrid? (4) If the plant were an introduced hybrid, were the two parents *L. amplexicaule* and *L. purpureum*? (5) If the plant had been introduced, had it previously been described? The study that ensued was designed to answer these questions and typifies standard methods of biosystematic analyses.

Materials and Methods

Descriptive notations and experimental taxa

Lamium amplexicaule L. and *L. purpureum* L. are diploid species (2*n* = 18) originating in Europe but widely distributed in North America. Both are winter annuals and are common weeds in moist, disturbed habitats, including irrigated fields and orchards of the Northwest. The flowering stems of both are erect or slightly spreading from the base; the leaves are opposite and deeply toothed or lobed. The primary distinguishing characteristics (*L. amplexicaule* vs. *L. purpureum*) are: leaves wider than long, rounded at the tip, and the upper sessile and not crowded nor pigmented vs. leaves longer than wide, acute, and all petiolate, the upper crowded and reddish pigmented; corolla tube 9-11 mm long, thrice as long as the upper lip, and corolla bright lavender in color vs. corolla tube 4-6 mm long, twice as long as the upper lip, and corolla pale lavender. The third taxon, referred to as *L. "hybridum"* for convenience, has leaves resembling *L. purpureum* but somewhat larger, more deeply lobed, less crowded above and only slightly pigmented; the flowers are intermediate in

size and shape but are colored similarly to those of *L. amplexicaule;* in habit, the plants are more robust, extensively branched and widely spreading. In the study areas (Figure 1), the three taxa occur sympatrically.

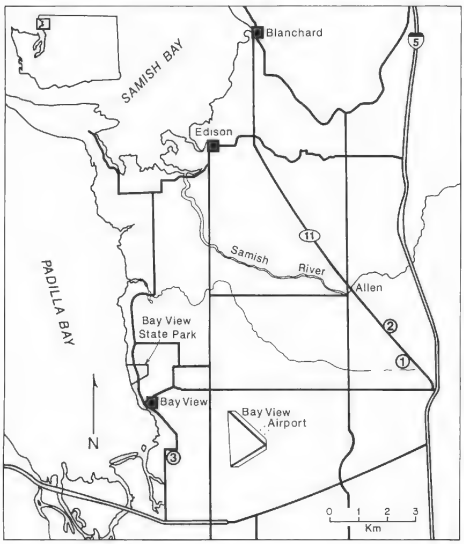

Figure 1. Map showing established populations of *Lamium hybridum* in Skagit County, Washington.

Field Sampling and Data Collection

In April, 1986, at the original site of observation (site 1, Figure 1), a transect was established through the most dense part of the population, paralleling highway 11. At five meter intervals along the transect, two 1-meter-square plots were located, one on each side of and one meter from the transect, for a total of 58 plots. Individuals of the three taxa were counted and frequency and abundance were calculated. Twenty suitably mature plants were collected along the transect, five of *L. purpureum,* four of *L. amplexicaule,* and eleven of *L. "hybridum."* These numbers were indicative of the relative abundance of the three taxa. In May of 1987 and again in 1989, additional collections were made from a dense sympatric population at site 2 (Figure 1). The purpose and nature of these collections are noted below under appropriate headings.

Morphological Measurements and Comparisons

A total of 24 morphological variables (listed in Table 1) was selected and measured on 60 specimens, 20 of each taxon. These specimens included the 20 plants collected from site 1 (and noted above), and 40 plants collected in 1989 along two 30 m transects at site 2. All plants selected for the analyses were in a similar stage of anthesis and measurements were made on fresh plants. The morphological relationships among the 60 specimens were determined using a principal components analysis (SPSSx 1984), the most common type of multivariate analysis in biosystematic studies.

Flavonoid Analyses

Thirty suitably mature plants, ten of each taxon, were randomly collected at site 2 in 1987. The flowers were removed and from these anthocyanins were extracted in 1% methanolic HCl. From the resulting extracts, anthocyanins were isolated, characterized, identified, and quantified using methods of paper chromatography as described by Taylor (1987), including spectral anslysis and hydrolysis. After the flowers had been removed, the plants were air dried, crushed, and flavonoid pigments were extracted in 80% methanol. Using standard methods of paper chromatography (Markham 1982) and spectral analysis (Mabry *et al.* 1979), the flavones and flavonols were isolated, characterized, quantified, and largely identified. Flavonoid (including anthocyanin) similarities (similarity values or SVs) among plants were determined by application of the formula: SV = similarities/similarities + dissimilarities (SV = s/s+d), first used by Sokal and Sneath (1963). The co-occurrence of a particular compound in two plants was given a similarity of three; an additional value of two was assigned if the compound was of the same scored concentration, one if the concentrations differed by a single scored value; Similarities + dissimilarities = 5. A pigment not occurring in either plant was not considered in determination of similarity. From these data, a covariance matrix (SPSSx 1984) was generated and used to construct a phenogram and dissimilarity triangle.

Flavonoids are the most widely used of all secondary metabolites in biosystematic studies. They are stable, can be analyzed from small

TABLE 1. Morphological variables used in comparative analyses.

1 – plant height (cm)
2 – mean leaf length (mm)
3 – mean leaf width (mm)
4 – length of stem (mid) leaf petiole (mm)
5 – upper leaves clasping = 1; non-clasping = 2
6 – depth of (mid) leaf margin incisions (mm)
7 – leaf venation pattern: interveinal space reduced and non-raised = 1; interveinal space med. and slightly raised = 2; interveinal space greater and more raised = 3
8 – leaf pubescence: sparse on both surfaces = 1; sparse on lower surface = 2; relatively dense on both surfaces = 3
9 – length of lowest internode (cm)
10 – calyx length (mm)
11 – calyx pubescence (character states: sparsely strigose = 1; moderately strigose = 2; sericeous = 3)
12 – calyx straight = 1; divaricate = 2
13 – corolla length (mm)
14 – corolla tube length (mm)
15 – galea length (mm)
16 – corolla color: pink = 1; lavender = 2
17 – color of galea pubescence: white = 1; white with pink base = 2; pink to purple = 3
18 – ring of hairs inside base of corolla tube: absent = 0; present = 1
19 – corolla pubescence (outside): absent = 0; sparse = 1; moderate = 2; heavy = 3
20 – filament pubescence: absent = 0; sparse = 1; moderate = 2; heavy = 3
21 – leaf blade orientation: parallel to stem = 1; perpendicular to stem = 2; varied = 3
22 – purple pigmentation of upper leaves: absent = 0; trace = 1; light = 2; moderate = 3; heavy = 4
23 – verticels of flowers per stem (number)
24 – branches per flowering stems (number)

samples, and can be tentatively identified by few procedures (Harborne and Turner 1984).

Cytological Observations

In 1986, seeds of *L. "hybridum"* were collected (by Joe Arnett) at site 1, germinated, and seedlings were grown to maturity in a greenhouse. Young anthers were excised from 20 immature flower buds and squashed in 2% aceto-orcein. From these buds, only one preparation showed meiotic figures clear enough to allow chromosomal counts. Several microsporocytes were examined and although precise counts were difficult, they consistently approximated $n = 18$ (Arnett, unpublished). As noted by Arnett and Bernstrom (1955) before him, suitable meiotic figures are difficult to obtain in *Lamium* because of very small chromosomes and few anthers. In June of 1988, seeds collected from plants of site 2 were germinated in petri dishes and root tip squashes were made of 10 seedlings each of *L. "hybridum"* and *L. amplexicaule*, and five of *L. purpureum*, the seeds of which were difficult to germinate. The squashes were stained with aceto-orcein and mitotic figures were examined. Finally, pollen samples of all plants used in morphological analyses were stained with acetocarmine, to get an estimation of viability, and measured.

Transplantations

Numerous specimens of all three taxa were transplanted from site 2 into an experimental garden at Western Washington University, Bellingham, WA. Also, seedlings of *L. "hybridum"* and *L. amplexicaule* were planted in the garden.

Isozyme Analysis

Ten flowering specimens of each taxon collected from site 2 in April of 1989 and ten specimens of *L. "hybridum"* from the experimental garden were sent to Washington State University for isozyme analysis. The analysis was done by Paul Wolf from the lab of Doug Soltis. Twelve enzymes or enzyme systems were surveyed electrophoretically.

Results and Interpretations

Population Structure

The percent frequencies and abundance (plants/sq. meter) of the three taxa at site 1 were: *L. amplexicaule* 17 and 0.12; *L. purpureum* 12 and 0.22; *L. "hybridum"* 76 and 2.29. Clearly, *L. "hybridum"* is more invasive or at least reproductively successful, an observation of potential consequence in dealing with northwest weeds. At site 2, although the population structure was not determined,

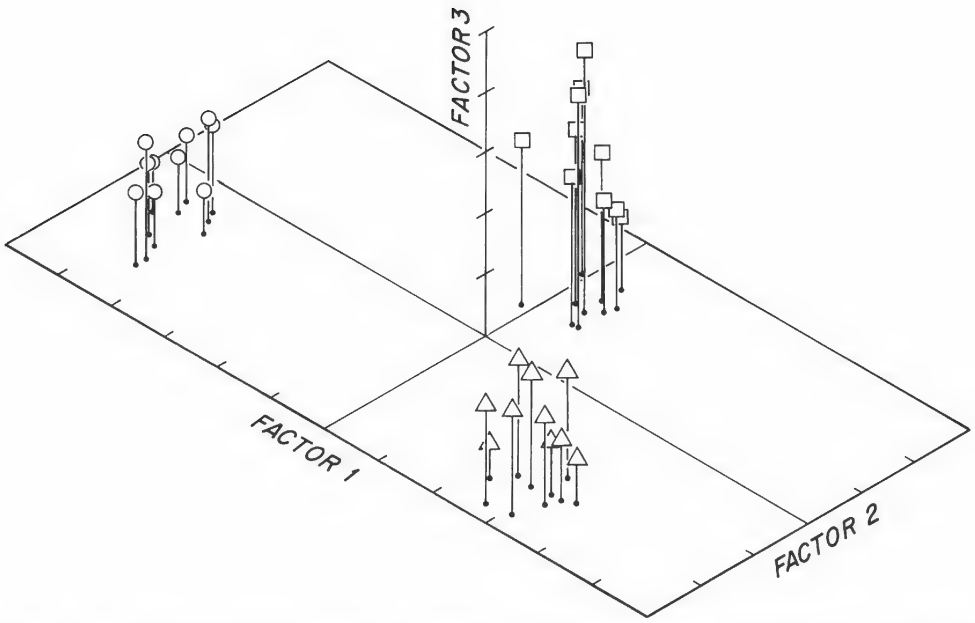

Figure 2. Ordination of odd-numbered plants based on principal components analysis; factors = components. Circle: *L. amplexicaule;* triangle: *L. purpureum;* square: *L. hybridum.*

L. "hybridum" appeared to be even more predominant.

Morphological Relationships

The principal components analysis shown in Figure 2 indicates the morphological relationships of the three taxa. Only the odd numbered specimens are plotted on the chart, including specimens from both collection sites. The analysis yielded six components with eigenvalues greater than one, indicating that the variables are moderately correlated (an inverse relationship exists between the number of components with high eigenvalues and the extent of correlation among variables). The first component (see Figure 2) accounted for 44.6% of the variance and separated *L. amplexicaule* from the other two taxa. The variables with the highest loadings, i.e., those that contributed most to the separation along component (factor) 1, listed according to loading values (high to low), were: upper leaves clasping vs. non-clasping (non-clasping in *L. amplexicaule* = *L.a.*); the presence or absence of a ring of hairs inside the corolla tube (absent in *L.a.*); pigmentation of upper leaves (non-pigmented in *L.a.*); calyx pubescence (sericeous in *L.a.*); corolla pubescence (heavy in *L.a.*); corolla tube length (longer in *L.a.*); and color of galea pubescence (pigmented throughout in *L.a.*). The second component accounted for 13.4% of the variance and separated *L. purpureum* from *L. "hybridum."* The variables with the highest loadings, from high to low, were: depth of leaf margin incisions (1/3 as deep in *L.p.*); leaf venation pattern (intervenal space less raised in *L.p.*); corolla pubescence (less dense in *L.p.*); branches per flowering stem (fewer or none in *L.p.*); and corolla length (shorter in *L.p.*). The third component accounted for 9.9% of the variance with only two variables having high loadings: leaf length and leaf width, both of which further separated *L. amplexicaule* (leaves longer than wide in *L. purpureum* and *L. "hybridum"* and vice versa in *L. amplexicaule*).

Perhaps the most significant result of the principal components analysis is the fact that the first component accounted for such a large proportion of the variance and that *L. amplexicaule* separated from the other taxa along this component. This suggests that the relationship between *L. purpureum* and *L. "hybridum"* is much greater than between *L. amplexicaule* and either or both of the other two

taxa. This pattern of relationship is graphically portrayed in Figure 2. The results, then, of the principal components analysis do not support the hypothesis that *L. amplexicaule* is a parental species of *L. "hybridum"* but do suggest that *L. purpureum* is.

Comparative Flavonoid Chemistry

A total of 28 flavonoid compounds, 10 of which were anthocyanins, was isolated and used in analyses. The characteristics, distribution patterns, relative concentrations, and tentative identifications of the 18 flavones and flavonols are presented in Table 2. The identifications, occurrence and relative concentrations of anthocyanins are presented in Table 3. *Lamium "hybridum"* combines the anthocyanins of the other two species, suggesting their parental status. However, the occurrence of the other flavonoids does not support this interpretation; *L. "hybridum"* much more closely resembles *L. purpureum*, both in the sharing of flavones and flavonols and in their relative concentrations. In fact, all compounds found in *L. purpureum* also occurred in *L. "hybridum."* The most likely scenario, then, considering the results of the flavonoid analyses in conjunction with other data, is that *L. "hybridum"* shares flavones and flavonols with *L. purpureum* because the latter is a parental species; it shares anthocyanins with *L. amplexicaule* because the second and unknown parental species was similarly pigmented with malvidin glycosides. Also the observation that two compounds were found only in *L. amplexicaule* and two were unique to *L. "hybridum"* further supports this scenario. The presence of a greater number of flavonoids in *L. "hybridum"* supports the hypothesis of allopolyploid origin. The results of the chromatographic analyses are depicted in the phenogram and distance triangle of Figure 3. The co-occurrence of the malvidin glycosides in *L. amplexicaule* and *L. "hybridum"* skews the relationship in that direction.

Cytological Determinations

Although restricted to a single plant, chromosomal counts of microsporocytes of *L. "hybridum"* showed that taxon to be tetraploid ($n = 18$). Precise chromosomal counts of root tip cells of germinating seedlings were difficult to make, but the results were unambiguous in terms of ploidy level. In *L. "hybridum,"* 25 mitotic cells from seven seedlings

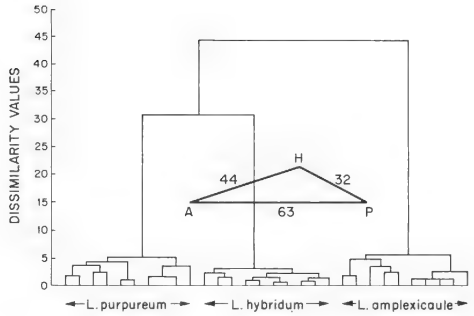

Figure 3. Phenogram and distance triangle showing relative similarities (dissimilarities) among experimental plants and species, based on flavonoid compounds. In the triangle, A = *L. amplexicaule*, H = *L. hybridum*, and P = *L. purpureum*.

were examined with a mean count of 34 ± 6 chromosomes. In *L. amplexicaule*, 19 cells from nine plants were examined with a mean count of 17 ± 3 chromosomes. In *L. purpureum*, 13 cells from five plants were examined with a mean count of 18 ± 2 chromosomes. These results are consistent with the published chromosome numbers of $2n = 18$ for *L. amplexicaule* and *L. purpureum*, diploid species. Also, this confirms that *L. "hybridum"* is a tetraploid, $2n = 36$. Pollen viability, based on stainability, was the same for all three taxa: 91 ± 7%, 90 ± 9%, and 91 ± 10%. The high pollen fertility (stainability) suggests that *L. "hybridum"* is an allopolyploid. However, Soltis and Soltis (1989) and Ness *et al.* (1989) have shown that autopolyploids may exhibit genetic equilibrium, thus high pollen fertility. Pollen grain size was significantly larger ($p = .05$) in *L. "hybridum"* as would be expected in a tetraploid. Relative mean sizes (length X width), standardized to 1, were: *L.a.* = 1.00, *L.p.* = 1.01, *L.h.* = 1.32.

Electrophoretic Analysis

From the twelve enzymes surveyed, 44 isozymes/allozymes were isolated; see Figure 4. Only two cases of heterozygosity within taxa were observed: one plant and one isozyme in each of the diploid species. The garden and field specimens of *L. "hybridum"* were homozygous for all isozymes. For convenience and because of this low percent of heterozygosity, the three taxa have been considered homozygous in Figure 4. Of the 44 isozymes, only four occurred in all three taxa; two were restricted

TABLE 2. Characteristics and Distribution Patterns of Flavonoids Compounds Isolated by Paper Chromatography.

Spot Number	Rf Values (BAW/HOAC)	Spot Appearance[1]		UV Spectrum[2]	Hydrolysate (Aglycone)	Tentative I.D.	Occurrence and Relative Concentration		
		UV	UV/NH_3	($AlCl_3$)			*amplex.*	*hybridum*	*purpureum*
1	40/53	PuAb	Y-OFl	257, 265s, 296s, 358 (430)	Quercetin	Q.3-rutinoside	+	++	++
2	42/13	PuAb	bYFl	255, 267s, 348 (423)	Luteolin	L.7-glucoside	++	++	++
3	57/27	PuAb	bYFl	254, 266s, 347 (424)	Luteolin	L-4',7-diglucoside	++	++	–
4	63/27	PuAb	Y-GFl	267, 336 (350, 383)	Apigenin	A-7-glucoside	++	++	+
5	58/45	PuAb	bY-F1	255, 268s, 297, 356 (431)	Quercetin	Q.3 (acyl)-glucoside	–	++	++
6	37/53	PuAb	YFl	256, 266s, 297, 357 (430)	Quercetin	Q.3-diglucoside	++	+	+
7	82/06	PuAb	Y-OFl	253, 267s, 289, 348 (420)	Luteolin	Luteolin	+++	+	+
8	82/28	PuAb	Y-GFl	265, 297s, 314, 355s (395)	Kaempferol	K.3 (acyl)-glucoside	–	+	+
9	28/10	PuAb	Y-GFl	265, 295s, 318, 360 (400)	Kaempferol	K. glycoside	+	–	–
10	43/38	PuAb	Y-OFl	263, 342 (weak)	– – –	A. glycoside (?)	++	++	+
11	63/13	YFl	bYFl	– – –	– – –	K. 4'-glucoside (?)	+	++	+
12	63/17	PuAb	YFl	– – –	– – –	– – –	+	+	+
13	60/39	PuAb	bYFl	254, 265s, 295s, 356 (430)	– – –	Q.3-glucoside	+	++	++
14	58/59	PuAb	Y-GFl	266, 285, 336 (350, 395)	– – –	A.7 (acyl)-rutinoside (?)	–	++	+
15	58/46	PuAb	Y-GFl	265, 295s, 337 (345, 392)	– – –	A.7-rutinoside (?)	–	+	+
16	38/11	YFl	YFl	– – –	– – –	Q.7-glucoside (?)	+	+	+
17	40/71	PuAb	YFl	– – –	– – –	– – –	+	–	–
18	84/39	PuAb	YFl	– – –	– – –	– – –	–	+	–

[1]Abbreviations: Ab = absorption, Fl = fluorescence, G = green, O = orange, Pu = purple, Y = yellow, b = bright.

[2]Wave lengths (nanometers) in methanol; the shift with addition of $AlCl_3$ is indicated in parentheses.

TABLE 3. Anthocyanins—Occurrence and Relative Concentration

Anthocyanin[1]	*amplexicaule*	*hybridum*	*purpureum*
Cyanidin 3,5-diglucoside	++	++	++
Cyanidin acyl-3 glycoside	+	++	++
Delphinidin 3,5-diglucoside	+	++	++
Delphinidin 3-glucoside	–	+	+
Delphinidin acyl-glycoside	–	+	+
Malvidin 3,5-diglucoside	++	+++	–
Malvidin 3 rhamnose, 5-glucoside	+	++	–
Malvidin acyl-glycoside	+	++	–
Malvidin glycoside (1)	+	+	–
Malvidin glycoside (2)	–	+	–

[1]Identifications were based on Rf values with several developing solvents, spectral analyses, stepwise hydrolysis, and comparisons with known standards (aglycones).

to *L. amplexicaule* and *L. "hybridum,"* suggesting possible parentage by the former; fourteen were restricted to *L. purpureum* and *L. "hybridum"* and none was unique to *L. purpureum*, thus strongly implicating *L. purpureum* as a parent; fifteen were unique to *L. amplexicaule*, sufficient evidence to reject this taxon as a parent; and nine were unique to *L. "hybridum,"* suggesting an undetermined second parent. In summary, then, *in situ* hybridization between the diploid taxa can be ruled out on the basis of enzyme electrophoresis. Also it is unlikely that a different source of *L. amplexicaule* was the second parent, given its high level of enzymatic distinction.

Discussion

Interestingly, in 1786 Villars discovered a population of plants which he considered to be intermediate between *L. amplexicaule* and *L. purpureum*. Accordingly, he named his discovery *Lamium hybridum*. Subsequently, the question of the origin of the taxon has been widely debated. The early taxonomic history of *Lamium hybridum* Vill. was outlined by Little and Warburg (1953), beginning with an original description by John Ray. These authors cite several references voicing diverse opinions concerning hybrid origin, with *L. amplexicaule* and *L. purpureum* most frequently named as the likely parents. Little concludes that the "balance of evidence" is against hybrid origin. Warburg, being a much later contributor to the article, had the advantage of more recent cytological data (e.g., the tetraploid status) and agrees that hybridization probably was involved but emphasizes that *L. hybridum* and other related taxa "must be treated as independent species." According to Hegi *et al.* (1936), there are two naturally occurring forms of *L. hybridum:* ssp. *intermedium* and ssp. *dissectum*. These authors noted that both subspecies are intermediate between *L. purpureum* and *L. amplexicaule*, ssp. *intermedium* most definitely so. However, taxonomic revision (Tutin *et al.* 1972) placed ssp. *intermedium* in the separate species, *L. moluccellifolium* Fries, and ssp. *dissectum* became a synonym of *L. hybridum*. The description of *L. hybridum* Vill. fits that of *L. "hybridum"* and from this point the two will be considered synonymous.

Several earlier studies have attempted to establish the parental species of *L. hybridum* (Bernstrom 1941, 1944, 1949, 1955; Jones and Jones 1965; Jorgensen 1927; Little and Warburg 1953; and others). All consider *L. purpureum* to be a parent but *L. amplexicaule* is questionable, both because of a lesser morphological similarity and apparent reproductive isolation based on attempts to hybridize the two diploids. The most comprehensive hybridization studies were carried out by Bernstrom (1955), involving several *Lamium* species. He crossed *L. purpureum* with *L. bifidum* (2*n*) and obtained a sterile F1 hybrid which he treated with colchicine to derive a synthetic allopolyploid. This he crossed with *L. hybridum* and obtained a fertile tetraploid with normal bivalent formation. He also produced a colchicine-derived autopolyploid of *L. purpureum* which he also

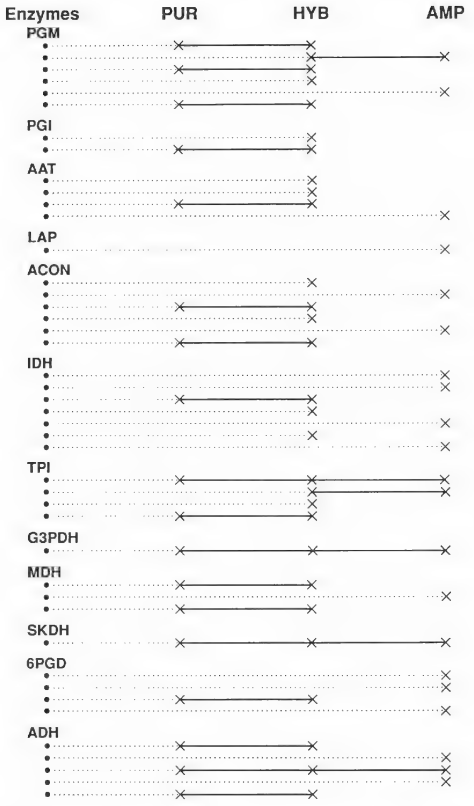

Figure 4. Distribution of 44 isozymes/allozymes as determined by enzyme electrophoresis. PGM = phosphoglucomutase, PGI = phosphoglucoisomerase, AAT = aspartate dehydrogenase, LAP = leucine aminopeptidase, ACON = aconitase, IDH = isocitrate dehydrogenase, TPI = triosephosphate isomerase, G3PDH = glyceraldehyde-3-phosphate dehydrogenase, MDH = malate dehydrogenase, SKDH = shikimate dehydrogenase, 6PGD = 6-phosphogluconate dehydrogenase, ADH = alcohol dehydrogenase.

crossed with *L. hybridum*. The result was a semifertile 4*n* hybrid which produced trivalents at meiosis, presumably due to three sets of chromosomes from *P. purpureum*. These results suggested that the parents of *L. hybridum* are *L. purpureum* and *L. bifidum*.

Conclusions

The questions asked in the introduction can be answered: (1) Is *L. "hybridum"* a hybrid species? The flavonoid, morphological, cytological, and electrophoretic data support this hypothesis, with *L. purpureum* being one of the diploid parents. (2) Is *L. "hybridum"* an allopolyploid? Certainly the cytological data in concert with the electrophoretic and other experimental results support this hypothesis. (3) Did hybridization occur *in situ*? The unescapable conclusion is that it did not. (4) If *L. "hybridum"* is an introduced hybrid, are the two parents *L. amplexicaule* and *L. purpureum*? The results of this study strongly suggest that *L. purpureum* is but *L. amplexicaule* is not. (5) Had *L. "hybridum"* previously been described? Yes, coincidently, it matches the description of *L. hybridum* Vill. and is similar to the few specimens of *L. hybridum* Vill. observed by the author at the U.S. National Herbarium (US), the University of Maryland (MARY), and the University of Massachusetts (MASS). A final question, then, would be: What species is the second diploid parent (assuming that only one additional species was involved, which perhaps is a bit presumptuous)? My data can not be addressed to this question, but the work of Bernstrom (1955) would suggest *L. bifidum*. In spite of my attempts, I have not yet been able to obtain seeds of this European species to test this hypothesis.

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Effects of Riparian Community Structure, Sediment Size, and Water Quality on the Macroinvertebrate Communities in a Small, Suburban Stream

Abstract

We studied the relationships between benthic macroinvertebrates, water quality, sediment characteristics, and riparian community structure in Padden Creek, a second-order stream in Bellingham, Washington, to look for patterns in the macroinvertebrate community structure between upstream and downstream sites. Padden Creek was sampled at four sites; one site was densely forested and relatively unpolluted, while the remaining sites were affected to various degrees by channelization, deforestation, and nonpoint source pollution. We measured water quality (including nutrients), sediment structure, riparian vegetation, and benthic macroinvertebrate densities at each site between 14 May and 1 October 1989. Many taxa were more abundant at the undisturbed, forested upstream site (Site 1), especially pollution intolerant mayflies, stoneflies, and caddisflies. At Site 2, where the surrounding forest had been cleared, there was a decrease in the density of shredders, predators, and collector-filterers, and an increase in scrapers. At Sites 3 and 4, where the stream is affected by organic pollution, there were fewer representatives from pollution intolerant orders (Ephemeroptera, Plecoptera, and Trichoptera) and many more non-insect taxa (e.g., oligochaetes and gastropods). Thus, the effects of channelization, deforestation, and pollution resulted in major changes in the structure of macroinvertebrate communities at downstream sites, suggesting that such riparian alterations imitate similar urbanization effects of higher-order rivers.

Introduction

Dense riparian vegetation influences the trophic structure of headwater streams by shading (which decreases autotrophic production) and by providing a large input of allochthonous detritus in the form of coarse particulate organic matter (CPOM). This loading, in turn, is reflected in the functional feeding group composition of benthic macroinvertebrates. Headwater sections of streams are typically populated by a large proportion of macroinvertebrate shredders, which shifts to higher proportions of scrapers in midreaches and collectors in lower reaches of river systems (Vannote *et al.* 1980, Hawkins and Sedell 1981). Other factors besides organic matter also affect the community structure of benthic macroinvertebrates, including changes in water quality, land use alterations, and changes in substrate characteristics (Hawkes 1979, Newbold *et al.* 1980, Williams 1980, Molles 1982, Kondratieff *et al.* 1984, Minshall 1984).

Padden Creek is a small, second-order stream that is typical of many urban streams in that portions of its watershed have been impacted by channelization, deforestation, and non-point source pollution. Our objectives were to evaluate the effects of changes in water quality, riparian community structure, and sediment size on the macroinvertebrate taxonomic structure and functional group composition in Padden Creek. In doing so, we hoped to illustrate some of the influences of urban development on stream biota.

Study Sites

Padden Creek begins as a lake outlet and flows 4.72 km from Lake Padden (elevation 136 m) to the marine waters of Bellingham Bay. The watershed, which occupies a total area of 15.5 km^2, includes Connelly Creek, the only tributary, and two small inlets of Lake Padden (Figure 1).

We studied four sites in Padden Creek, which are described in Table 1. Site 1 was surrounded by dense, second-growth forest, and had a rocky, diverse substrate. Site 2 had a comparatively open canopy due to urbanization and a homogeneous substrate due to channelization of the stream. Connelly Creek enters between Sites 2 and 3, and was the major source of nutrient pollution into the creek. Site 3 was in a park (Fairhaven Park), which

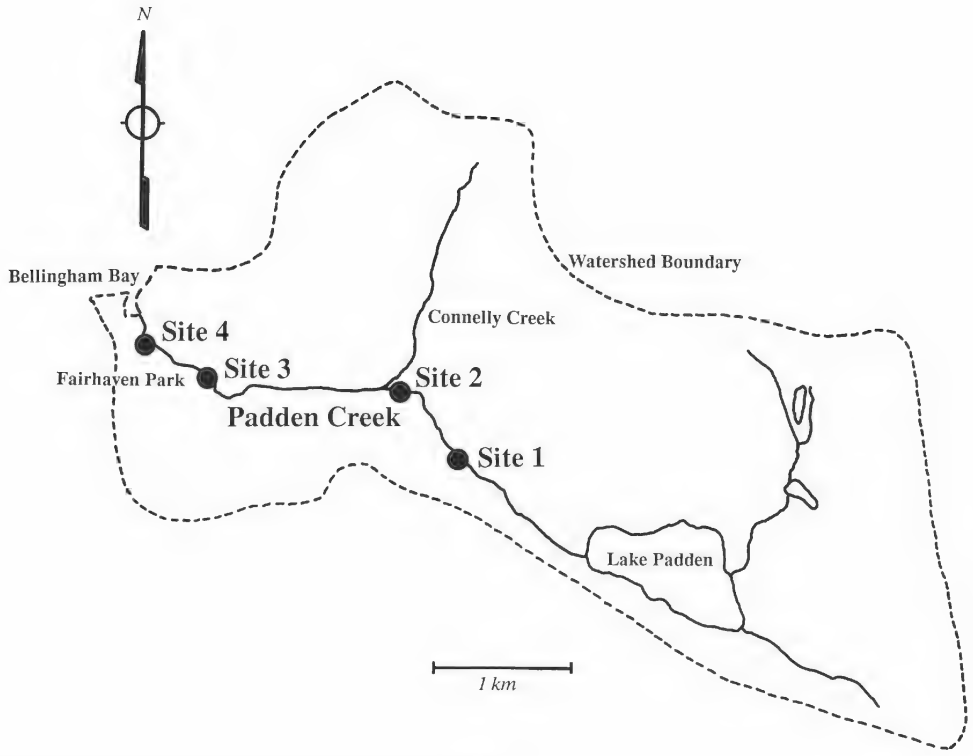

Figure 1. Padden Creek sampling sites and watershed description.

TABLE 1. Descriptions of Padden Creek sampling sites.

Factor	Site 1	Site 2	Site 3	Site 4
nutrient concentrations	low-moderate	low-moderate	elevated	elevated
riparian vegetation	second-growth coniferous forest	alder, gaps in canopy	park-like vegetation	freshwater wetland
stream velocity	fast-flowing	fast-flowing	fast-flowing	slow-flowing
substrate	diverse cobble-pebble	uniform cobble-pebble	diverse pebble-sand	diverse pebble-sand
stream gradient	61 m/km	19 m/km	8 m/km	11 m/km

was forested and had a diverse substrate, but had poor water quality. Site 4 was located near the mouth of Padden Creek in a freshwater wetland, and was characterized by poor water quality, high turbidity, and a fine-grained substrate.

Methods

Four sites were sampled along the stream, as shown in Figure 1. The riparian vegetation was sampled on 14 April and 14 August, 1988. All tree species and common understory species in the riparian zone were identified, and the dominant tree species were determined by canopy cover. Stream sediment samples were collected on 10 August from a 929 cm^2 (1 ft^2) area to a depth of about 7.5 cm. The sediment samples were oven dried, sieved,

and weighed to determine sediment size fractions (Minshall 1984). Water samples were collected approximately monthly between 14 May and 1 October, 1988 at each Padden Creek site and from Connelly Creek where it joins Padden Creek. Water temperature was measured in the field. Laboratory analyses (pH, alkalinity, conductivity, turbidity, ammonia, nitrite/nitrate, soluble reactive phosphate, and total phosphorus) were done by the Institute for Watershed Studies (Western Washington University) using standard EPA protocols (EPA 1983).

Benthic macroinvertebrate samples were collected monthly between 14 May and 1 October using a Surber sampler (1 mm mesh size). Ten replicates were collected at each site on each date. The macroinvertebrates were preserved (in the field) in 10% formalin, sorted, and identified to the lowest practical taxonomic unit. Representative taxa were preserved in 70% ethanol. Macroinvertebrate densities were calculated for each taxa as the average number of individuals per square meter ($n = 10$ per site and taxa). In addition to the quantitative samples, insect emergence was noted, and log debris and larger rocks were sampled qualitatively. The qualitative data were not used in the calculations of macroinvertebrate densities, but were added to the taxonomic list.

Results and Discussion

Riparian Community, Stream Substrate, and Water Quality

Site 1 is dominated by dense, second-growth, coniferous forest about 90-100 years in age. The most common tree species include western hemlock (*Tsuga heterophylla*), red alder (*alnus rubra*), western red cedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*). The understory contains many hydrophytes such as devil's club (*Oplopanax horridum*) and skunk cabbage (*Lysichitum americanum*) that indicate water saturation of the soils near the creek. Other common understory species include vine maple (*Acer circinatum*), salmonberry (*Rubus spectabilis*), and sword fern (*Polysitchum munitum*). The riparian community at Site 2 is disturbed, and consists primarily of young alders and willows (*Salix* spp.) on one or both sides of the creek, as well as blackberries (*Rubus* spp.) and reed canary grass (*Phalaris arundinacea*). The forest at Site 3 in Fairhaven Park has a much more open canopy and understory than Site 1. The dominant tree species at Site 3 are bigleaf maple and red alder. Shrubs dominate the understory, especially snowberry (*Symphoricarpus albus*), ocean spray (*Holodiscus discolor*), and Indian plum (*Osmaronia cerasiformis*), indicating drier conditions than at Site 1. In the wetland area at Site 4, willows and alders form a dense canopy that overshadows much of the creek. Parts of the wetland are characterized by emergent aquatic species such as cattail (*Typha latifolia*) and bullrush (*Scirpus silvaticus*).

The gradient of a stream is one of the major factors controlling stream velocity and sediment size (Richards 1982). As the stream gradient decreases downstream, the mean sediment size usually decreases. Accordingly, the particle size in the riffles of Padden Creek shifted from a mixture of cobbles and pebbles upstream to mostly smaller pebbles downstream (Figure 2). At the same time, the weight of the fine sediment fraction (granule to sand) increased downstream. The only major exception to this was at Site 2. At this site the stream is channelized, which creates a more uniform stream velocity, particularly when viewed horizontally across the stream channel. As a result, the sediment structure at Site 2 is relatively uniform.

Because Padden Creek was at least partly shaded at all sampling sites, stream temperatures were consistently low. The highest temperature in Padden Creek (15.8°C) was measured downstream from the inflow of Connelly Creek on 24 August. Connelly Creek was not shaded at the sampling site and had noticeably higher water temperatures than Padden Creek (Table 2). Similarly, the values for pH, alkalinity and conductivity in Connelly Creek were much higher than at Sites 1 and 2 in Padden Creek. The influence of Connelly Creek can be seen at Sites 3 and 4, where the pH, alkalinity, and conductivity values are intermediate between those for Connelly Creek and the upstream sites of Padden Creek.

Ammonia concentrations were about the same at Site 3 as at Sites 1 and 2, and only slightly elevated at Site 4, even though ammonia inputs from Connelly Creek were high. Ammonia is usually transformed rapidly in streams to nitrate (Hynes 1974), suggesting that the elevated nitrite/nitrate concentrations at Sites 3 and 4 were probably caused by both ammonia and nitrite/nitrate inputs from Connelly Creek. Soluble reactive phosphorus concentrations were higher at Sites 3 and 4; however, total phosphorus concentrations were not.

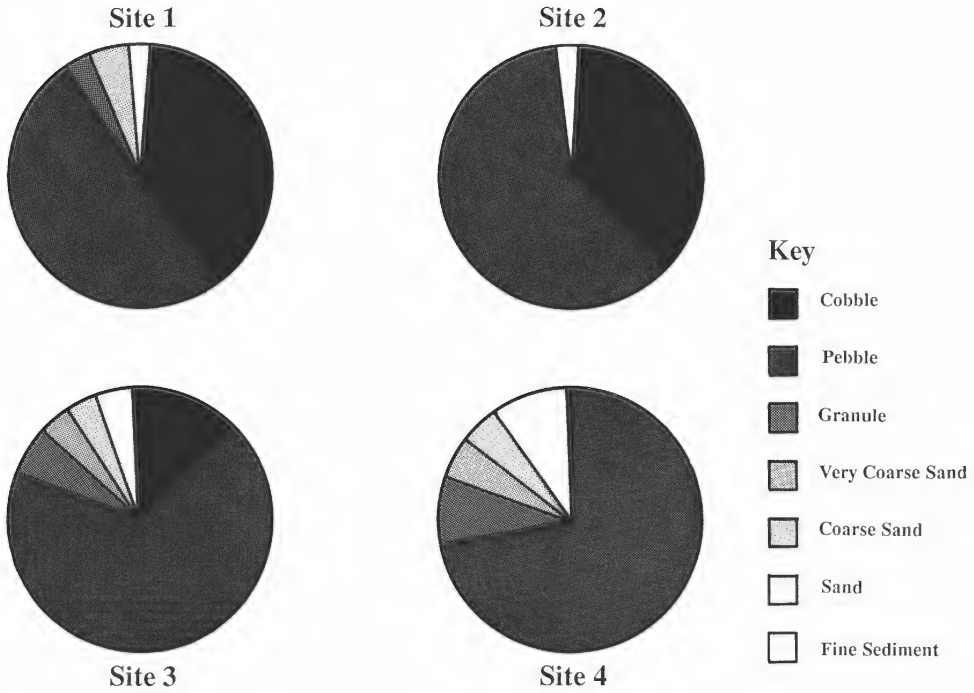

Figure 2. Padden Creek sediment size distribution (by percent of total weight), 10 August, 1988.

TABLE 2. Water quality data from Padden Creek and Connelly Creek.[1]

Parameter	Padden Creek–Data Ranges (Average)				Connelly Creek
	Site 1	Site 2	Site 3	Site 4	
Temperature (°C)	11.5-14.4	12.0-14.5	12.0-15.0	11.5-14.0	14.0-18.5
pH	7.43-7.70 (7.57)	7.47-7.59 (7.53)	7.70-7.84 (7.79)	7.76-7.91 (7.86)	7.85-8.53 (8.10)
Alkalinity (mg $CaCO_3$/L)	24.8-31.1 (28.7)	25.1-36.1 (32.2)	45.0-63.3 (55.3)	39.4-66.4 (56.1)	79.9-133.4 (99.8)
Conductivity (μS/cm)	96-109 (104)	97-113 (108)	134-175 (161)	136-184 (167)	218-353 (263)
Turbidity (NTU's)	3.1-6.3 (4.8)	2.8-7.3 (4.1)	2.7-4.8 (3.8)	3.1-4.7 (3.9)	2.8-5.4 (4.0)
Ammonia (μg N/L)	<2-33.7 (10.0)	<2.-19.7 (8.5)	<2-23.3 (6.8)	<2-28.9 (17.4)	12.1-556.5 (252.3)
Nitrite/Nitrate (μg N/L)	108.7-412.6 (280.4)	101.6-382.1 (267.3)	203.9-706.9 (393.8)	196.6-759.9 (392.0)	246.8-571.1 (417.4)
Sol. Phosphate (μg P/L)	5.0-14.4 (9.9)	6.1-13.6 (10.9)	13.2-29.5 (22.6)	14.3-28.7 (22.1)	22.5-45.7 (32.9)
T. Phosphorus (μg/L)	19.5-73.4 (28.0)	19.3-55.2 (39.8)	27.5-40.1 (34.1)	23.5-36.7 (33.6)	42.4-70.1 (52.8)

[1]The Padden Creek samples were collected from 14 May-1 October, 1988 (n = 5); Connelly Creek samples were collected from 21 June-1 October, 1988 (n = 4).

The exact sources of pollution to Connelly Creek have not been identified, but they are most likely the result of nonpoint source agricultural and residential runoff. The periodically high ammonia concentrations suggest agricultural runoff or faulty septic tanks. Along Connelly Creek, there are septic tanks as well as an intensively used agricultural area where manure is spread on the fields.

Benthic Macroinvertebrate Populations

We collected a total of 71 taxa from Padden Creek (the Padden Creek taxa list is available upon request from the authors), of which 21 taxa were defined as "common" (representing at least 1% of the total density at any site). Because downstream drift can affect interpretations of taxa distribution data, especially for rare taxa (Waters 1972), most of our discussion is restricted to the common taxa. Uncommon taxa that are especially sensitive to changes in the environment or those with special habitat demands are also discussed.

Many mayflies, stoneflies, and caddisflies preferred Sites 1 and 2. These three groups together made up 62-67 percent of the macroinvertebrate densities at the upstream sites, but only 40 percent at Site 3 and 26 percent at Site 4. Mayflies, stoneflies, and caddisflies are generally intolerant of pollution, especially the heptageniid mayflies and most stoneflies. Many other stream studies have reported similar patterns, i.e., decreases in mayflies, stoneflies, and caddisflies in polluted sections (e.g. Hynes 1970a, 1970b; Hawkes 1979; Wiederholm 1984).

A few mayfly genera, such as *Baetis* and *Paraleptophlebia,* are widespread and include species that can tolerate moderate pollution (Merritt and Cummins 1984). These two genera were relatively abundant at all four sites in Padden Creek. Some non-insect groups, on the other hand, actually prefer organically-enriched streams. In Padden Creek, these included amphipods, annelids, and molluscs; all of which were more common in the downstream sites. This distribution was especially true for the molluscs, which were not found at Site 1.

Many of the uncommon taxa also preferred Site 1. These included the stoneflies *Pteronarcys, Perlomyia, Despaxia augusta, Calineuria californica,* and *Hesperoperla pacifica;* the mayflies *Cinygma* and *Rhithrogena;* the caddisflies *Allocosmoecus partitus, Apatania sorex, Ecclisomyia, Neophylax,* and *Lepidostoma;* and the aquatic beetles *Hydrochus squamifer* and *Lara avara.*

Many predatory taxa also preferred Site 1, including the large, predatory stoneflies, *Hesperoperla pacifica* and *Calineuria californica.* These stoneflies consume large percentages of the standing crop of benthic invertebrates (Siegfried and Knight 1976). At Site 2, where the large stoneflies were absent, the medium-sized stonefly *Skwala* appeared to be the major invertebrate predator. At Sites 3 and 4, the largest insect predators were alderflies (*Sialis*). The filter-feeding *Parapsyche,* common at Site 3, may also be predatory. The predacious aquatic beetles *Agabinus sculpturellus, Agabus,* and *Hydrovatus* were among the few invertebrates with an apparent preference for Site 4. Species belonging to this family are very adaptable, and some of them occur in slow-flowing streams and lentic habitats (Usinger 1971). They may prefer Site 4 because the stream velocity is relatively slow and pool areas are relatively large.

Distribution of Hydropsychidae

The caddisfly family Hydropsychidae includes species that can tolerate moderate pollution (Hawkes 1979, Wiederholm 1984). In Padden Creek, this family showed a distinct longitudinal distribution pattern: *Hydropsyche* was more common at the upper sites and *Parapsyche* was more common downstream.

The longitudinal distribution of Hydropsychidae has been the subject of several studies in the eastern United States (Gordon and Wallace 1975, Wiggins and Mackay 1978). Most studies show that *Parapsyche* are found mostly in the upper headwater streams, while species of *Hydropsyche,* although widely distributed, tend to prefer downstream sections of rivers. These distributions are usually explained by differences in morphology: *Parapsyche* is a big caddisfly, having a coarse net that enables it to catch coarse particulate organic matter (CPOM), the major food source in headwater streams. Conversely, *Hydropsyche* larvae are small and build nets with a smaller mesh size than *Parapsyche* in order to feed on fine particulate organic matter (FPOM).

Our data could reflect the influence of Lake Padden, which has an epilimnetic outfall and probably adds FPOM to the upper section of the creek, thus favoring *Hydropsyche.* However, it is also possible that the *Hydropsyche* species inhabiting Padden

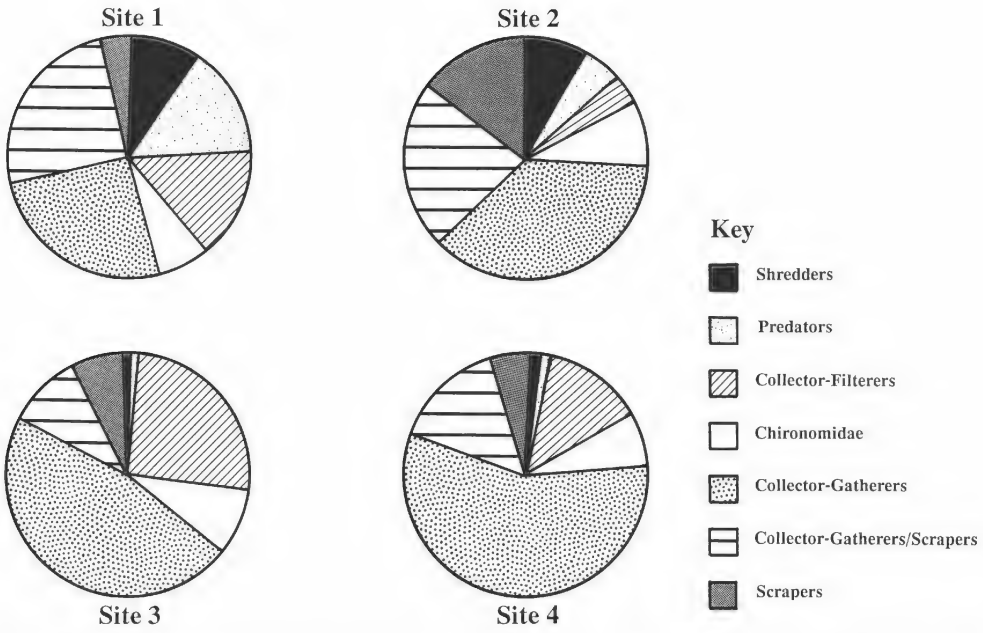

Figure 3. Padden Creek macroinvertebrate functional group distributions (percent of total density), 14 May-1 October, 1988.

Creek are less tolerant to organic enrichment than *Parapsyche* so that they are confined to the relatively unpolluted upstream portions of the creek.

Macroinvertebrate Functional Groups

Figure 3 summarizes the functional group percentages for the common taxa in Padden Creek (based on Merritt and Cummins 1984). Chironomid larvae were classified separately because species of Chironomidae belong to several different functional groups. Some mayflies are able to feed both as collector-gatherers and as scrapers; these taxa were classified as collector-gatherers/scrapers.

According to the River Continuum Concept (Vannote *et al.* 1980), Padden Creek is a headwater stream, characterized by a closed forest canopy, with its primary energy source coming from allochthonous organic matter in form of CPOM. Shredders, who feed on CPOM, should be abundant, while scrapers and collectors (who feed on periphyton and FPOM), should be less abundant. Although shredder densities were relatively low in Padden Creek compared to headwater streams sampled in western Oregon (Hawkins and Sedell 1981), shredders were proportionately more abundant at Site 1 than at the other Padden Creek sites. Padden Creek also is undoubtedly influenced by inputs of FPOM from Lake Padden, which probably caused the relatively high collector-gatherer and collector-filterer densities at all sites. The collectors were mainly represented by the filter-feeding caddisfly *Hydropsyche*, which was common at Site 1, and oligochaetes (collector-gatherers), which were common at all sites. Studies in England (Armitage 1978) and in Colorado (Ward and Short 1978) in creeks downstream from reservoirs also showed elevated populations of oligochaetes.

At Site 2, collector-gatherers and scrapers were the dominant functional groups. Predator and collector-filterer densities were much lower than at Site 1. Shredder densities and the number of shredder taxa were also slightly lower at Site 2 than at Site 1. The changes observed between Site 1 and Site 2 probably were caused by channelization, which reduced substrate heterogeneity (see Figure 2), and by deforestation, which increased the amount of light reaching the stream bed and changed the character of the riparian vegetation.

Minshall (1984) and Williams (1980) report that species diversity generally increases with

substrate heterogeneity. At Site 2, where the substrate was fairly homogeneous, there was a general reduction in species diversity, especially for predators and collector-filterers, from that found at Site 1. In an experiment with artificial substrates in a third-order stream in Ontario (Williams 1980), all predators showed a significant preference for areas having highly heterogeneous substrates.

Compared to Sites 1 and 2, Sites 3 and 4 had very unbalanced distributions of functional groups. Predator and shredder populations were greatly reduced at Sites 3 and 4, while collector-filterers were increased at Site 3 and collector-gatherers were increased at Site 4. Scraper populations had similar densities to those at Site 1, but consisted of different taxa. These differences probably were correlated with the decrease in substrate size and slower stream velocities at Site 4, which favors collector-gatherers more than filter-feeders. In addition, the changes in water quality may have contributed to shifts toward relatively tolerant taxa at Sites 3 and 4. Similar patterns are described by Wiederholm (1984), who reported that the expected longitudinal (downstream) succession of macroinvertebrate functional groups is altered in nutrient-enriched streams because of the change in algal flora and increase in detritus input caused by eutrophication.

Conclusions

Many Padden Creek taxa, especially mayflies, stoneflies, and caddisflies, were more abundant at Site 1, which was densely forested, had a heterogeneous substrate, and was relatively unpolluted. The downstream sites, which were affected by channelization, deforestation, pollution, and natural decreases in sediment size and stream velocity, were populated mostly by tolerant taxa and had a greater proportion of non-insect taxa than the upstream sites.

All macroinvertebrate functional groups were well represented at Site 1. The relatively high density of shredders at that site suggests that CPOM was a major food source. In addition, the addition of FPOM from Lake Padden resulted in large numbers of collector-gatherers and collector-filterers at all sites. Channelization at Site 2 caused a decrease in the number and density of predators and collector-filterers. Because the riparian forest was partly cleared at this site, the number of shredder taxa also was decreased. Scraper densities, on the other hand, increased because as more light reached the stream, algal productivity probably increased. Relatively tolerant insect and non-insect taxa, most of which were collector-filterers and collector-gatherers, dominated Sites 3 and 4, where pollution from Connelly Creek and reduced sediment size and stream velocity may have been major factors influencing the macroinvertebrate community structure. Shredders and predators were very uncommon at both downstream sites.

Our study showed that changes in water quality, substrate characteristics and land use are associated with longitudinal zonation of the benthic invertebrate community in Padden Creek. Because of interactions between these factors and the biota, the importance of each single factor cannot easily be quantified. However, there was a general tendency for channelization and deforestation to mimic the habitat found in mid-reach rivers, resulting, at Site 2, in a greater density of scrapers than would normally be expected in a headwater stream. Similarly, at Sites 3 and 4, the combined effects of deforestation, nutrient inputs, and natural decreases in the stream velocity and substrate size created a habitat similar to that found in lower reaches of rivers, resulting in a macroinvertebrate community dominated by collector-gatherers and collector-filterers.

This study was relatively qualitative in nature, being limited by time, funding, and lack of a preexisting data base on the stream. Its primary purpose was to collect baseline data on the macroinvertebrate taxa in Padden Creek, and to look for general longitudinal trends. These objectives were met, despite the design constraints, suggesting that stream ecosystem studies are not restricted to multiyear, externally-funded projects. Land-use changes along streams are commonplace, and increased development pressure will likely result in additional changes along stream courses in the Pacific Northwest. Further research should emphasize appropriate biological and chemical sampling that may lead to a comprehensive monitoring of impacts on streams. Our study suggests that very meaningful information can be gained from short-term sampling along stream gradients to assess impacts of land use patterns.

Acknowledgments

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Relationships Among Coyote Food Habits, Prey Populations, and Habitat Use

Abstract

A study of coyotes (*Canis latrans*) and prey relationships was conducted on the National Bison Range in western Montana from July 1974 to July 1975; additional unpublished data were used for the period 1972-1974. Scat analyses revealed that voles (*Microtus* spp.) were the most important food source throughout the year. During spring and early summer young native ungulates were important. Insects and fruit occurred most frequently in scats during late summer. Results of small mammal trapping in four habitats and observations of hunting coyotes indicated that coyotes hunted in habitats with greater vole population densities. Voles were apparently more vulnerable to coyotes because deer mice (*Peromyscus maniculatus*) were trapped more frequently in all four sampled habitats. These results show that even "generalist" predators such as coyotes modify their hunting to suit local conditions, often favoring small areas where seasonally favored prey species concentrate.

Introduction

Recent studies of coyote (*Canis latrans*) food habits have attempted to relate diet to social organization of coyotes (Ozoga and Harger 1966, Bekoff and Wells 1980, Bowen 1981), predator density (Clark 1972), habitat (Fichter *et al.* 1955, Ozoga and Harger 1966, Litvaitis and Shaw 1980, Andelt *et al.* 1987), and prey density (Korschgen 1957, Clark 1972, Johnson and Hansen 1979, Todd *et al.* 1981, Hamlin *et al.* 1984, Andelt *et al.* 1987). The coyote is considered a generalist predator, its diet usually reflecting the relative densities or biomass of prey species available (Clark 1972, Andelt *et al.* 1987). However, predator preference and prey availability (density and vulnerability) may affect both the proportion of a prey species eaten and the habitat in which the predator hunts (Murdoch 1969). This study examined: 1) composition of coyotes' diet, 2) the relative densities of cricetid rodents in four habitats, 3) the combined influence of vulnerability and preference on the coyotes' diet, and 4) the relationship between habitat use by voles and hunting coyotes.

Study Area

The National Bison Range is located near the southern end of the Flathead Valley in western Montana, and encompasses more than 7700 ha. Elevations range from 696-1361 m, and much of the southern half of the area is composed of small, rugged rocky canyons. Most observations were made on the northern half, where grasslands predominate and low ridges separate small basins. I estimated 9-13 adult coyotes inhabited the area during this study (Reichel 1976).

Methods and Materials

Field work was carried out from July 1974 through July 1975, and was supplemented with data from files of the National Bison Range (Anon. 1956-75). Four habitats were distinguished on the study area: grassland basin, grassland slope, brushy dry wash, and riparian. I observed coyotes hunting on 64 occasions for a total of 14 hours ($\bar{x}$ = 11.5 minutes, s = 9.02), and recorded the time they spent in each habitat. All observations used in the analysis were made in the north half of the study area, either from the road or repeatedly visited high elevation observation points. To determine habitat availability for hunting coyotes, the percentage of each habitat visible was estimated from each observation point. The habitat is moderately uniform; the range of percentages of each habitat visible from all observation points is reported.

Rodent populations were sampled monthly July-November 1975 and April-July 1976 using snap traps. Thirteen stations were randomly placed in each of four habitats and relocated during each month for a total of 117 trapping locations per habitat. Stations were placed >0.2 km apart and consisted of four snap traps placed within 1 m of a stake. Traps were prebaited for 2 days, set and checked daily the 4 following days. Within the 4 habitats the distance from a station to an adjacent habitat varied due to physical characteristics of each habitat. Stations in grassland basins and

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slopes were >0.2 km from adjacent habitats, in riparian habitats were >0.1 km from adjacent habitats, and were 1-10 meters from adjacent habitats in brushy dry washes.

Scats were gathered biweekly during May, June and July and monthly the rest of the year along a 72 km fixed route to insure only scats from a known time period were analyzed. Scats were washed and air dried in the laboratory. Mice were identified to genus using tooth characteristics (Hoffmann and Pattie 1968). Hair of other mammals was identified by comparison to reference specimens using standard identification techniques (Moore *et al.* 1974).

The relative importance of each prey species in the coyotes' diet was estimated by calculating the percentage of scats in a time period that contained the prey item (percent frequency). The G test (Sokal and Rohlf 1981) was used to test the distribution of: 1) the number of voles and deer mice trapped and, 2) number of voles between habitats.

I measured the proportionate difference (c) between the ratios of the populations of two prey species and the use of those species by coyotes, using Murdoch's (1969) equation c = (P1/P2)/(N1/N2) where P1 = proportion of the diet constituted by the first prey species; P2 = proportion of the diet constituted by the second prey species; N1 = population of the first prey species; and N2 = population of the second prey species. The proportionality constant c reflects two basic properties of predator-prey interactions: 1) the relative vulnerability of prey, and 2) predator preference for a prey species (Murdoch 1969).

Results and Discussion

Coyote Food Habits in Relation to Prey Populations

Analyses of 593 coyote scats collected during this study and 347 collected prior to it from fall 1972 to spring 1974 (G. P. Hallsten, C. Smith, and M. Vivion, unpubl. data), indicate that rodents were the most numerous prey items in the coyotes' diet. Voles (*Microtus montanus, M. longicaudus,* and *M. pennsylvanicus*) accounted for over 80 percent of the rodents (Table 1). In California (Ferrel *et al.* 1953, Hawthorne 1972) and Yellowstone National Park (Murie 1940) voles were also the most common food of coyotes. Numerous other workers have found that voles followed lagomorphs and/or deer in importance (Ogle 1971, MacCracken and Hansen 1982). Mountain cottontails (*Sylvilagus nuttallii*) were rare on the study area.

TABLE 1. Percent frequency of occurrence of items found in 940 coyote scats collected during fall 1972-summer 1975.

	Fall (n=315)	Winter (n=250)	Spring (n=211)	Summer (n=164)
Voles	79.4	88.8	74.9	40.8
Deer mice	4.7	2.8	0.5	2.4
Other rodents	7.9	10.0	11.8	14.1
TOTAL RODENTS	88.2	91.6	82.0	53.7
Deer	9.8	6.2	18.3	24.4
Pronghorn	1.6		10.9	1.8
Other ungulates	5.4	11.0	10.0	7.3
TOTAL UNGULATES	16.8	17.2	39.2	33.5
LAGOMORPHS	1.6		2.4	2.4
OTHER MAMMALS	1.9	0.8	0.4	7.4
BIRDS AND EGGS	6.6	7.6	12.4	19.5
REPTILES AND AMPHIBIANS			4.3	6.1
SEEDS AND FRUIT	1.0	0.4	0.5	30.5
INSECTS	2.2	0.8	7.1	30.5
UNKNOWN	3.8	4.8	1.9	1.8

Trapping data collected over the past 20 years suggested that vole populations were at low levels during this study (P. L. Wright, pers. comm., Reichel 1976). Voles were an important part of the coyote diet in Lava Beds National Monument, California, during years of both high and low populations (Bond 1939). Bond attributed this to the existence of local concentrations where coyotes can find voles even during periods of low populations. In contrast, voles were an important food source only during high population years in eastern Montana (Hamlin *et al.* 1984).

Nine times more deer mice (n = 680) than voles (n = 76) were trapped during my study ($G = 444$, $p < 0.01$, 1 df). Deer mice are more susceptible to trapping than voles (Nabholz 1973, Barbehenn 1974, Golley *et al.* 1975), however it is unlikely that different capture rates account for the c value of 260 between voles and deer mice (Table 2). The relative frequency of voles and deer mice in the coyote diet is not simply the result of gross habitat use differences between prey species (Table 3) because in each habitat more deer mice were captured than voles.

Other small mammals were relatively unimportant food items on the study area (Table 1). Birds and bird eggs occurred in coyote scats most

TABLE 2. Comparison of prey species to determine c values.

Species pairs	$\frac{N1^a}{N2}$	$\frac{P1}{P2}$	c
Microtus	1.05	.698	259.56
Peromyscus	8.59	.022	
Elk	82	.003	1.40
Bison	307	.008	
Bighorn Sheep	46	.030	25.03
Bison	307	.008	
Deer	360	.190	20.25
Bison	307	.008	
Pronghorn	108	.051	18.12
Bison	307	.008	
Bighorn Sheep	46	.030	17.83
Elk	82	.003	
Deer	360	.190	14.43
Elk	82	.003	
Pronghorn	108	.051	12.91
Elk	82	.003	
Deer	360	.190	1.12
Pronghorn	108	.051	
Bighorn Sheep	46	.030	1.38
Pronghorn	108	.051	
Bighorn Sheep	46	.030	1.24
Deer	360	.190	

[a]Mouse population figures are number trapped/100 trap nights; ungulate populations (total numbers) are for March 1975 (Anon. 1956-75).

frequently during spring and summer in this study (Table 1). Insects and fruits were most important during late summer (Table 1).

Deer (*Odocoileus virginianus* and *O. hemionus*) and pronghorn (*Antilocapra americana*) were most frequently eaten during late spring and early summer. Other native ungulates including bison (*Bison bison*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*) were used sporadically throughout the year (Table 1). Big game populations are counted during an annual census of the entire study area which is completely enclosed (Anon. 1956-75). The proportionality constant *c* was calculated for all species pairs based on early March 1975 populations (Table 2). It seems unlikely that differences in *c* would be due to predator (taste) preference for certain ungulate prey species, thus variation in *c* is most likely due to prey vulnerability. Differences in *c* values indicate large ungulates (bison and elk) were not as vulnerable to coyotes as small ungulates (pronghorn, deer, and bighorn sheep); the differences in vulnerability within each of the two size classes are small. It seems likely that elk and bison are taken exclusively as carrion; if substantial numbers of young were being killed, a peak in spring would be expected. Conversely, the 12-25 fold differences in vulnerability between large and small ungulates, and the strong peak of small ungulates in late spring and early summer diets, suggest that coyotes are killing substantial numbers of young pronghorn, deer, and bighorn sheep. The mortality rate of pronghorn fawns (<6 months) was 72 percent during 1974-75 and coyote predation contributed to this mortality (Reichel 1976).

Habitat Relationships of Coyotes and Voles

More voles were trapped in riparian habitat than in brushy dry washes ($G = 12.99$, $p < 0.01$, 1 df), and in brushy washes than in grassland basins ($G = 9.89$, $p < 0.01$, 1 df) or slopes ($G = 9.89$, $p < 0.01$, 1 df). There was little difference in the number trapped between grassland basins and slopes.

Coyotes hunted in riparian and brushy wash habitats a higher percentage of time than the maximum available percentages of those habitats;

TABLE 3. Observed habitat use by hunting coyotes (based on 64 observations totaling 842 minutes) compared to habitat percentages from observation locations, relative use (% use ÷ % availability) and mouse captures per 1000 trap nights in four habitat types. Trapping was conducted monthly July-November 1975 and April-July 1976.

	Coyote			Mouse Captures	
Habitat	Availability %	Use %	Relative Use	Voles	Deer mice
Grassland slope	45-55	25	0.5-0.6	1.93	87.71
Grassland basin	35-45	32	0.7-0.9	1.94	79.53
Brushy wash	1-4	8	2-8	14.19	78.28
Riparian area	0-10	34	3.4-34	24.85	98.39

grassland basins and slopes were used less than the minimum available (Table 3). Because observing coyotes was more difficult in riparian and brushy wash than in grassland habitats, it is likely that these differences are underestimated.

The relative habitat use by coyotes is identical to the ranking of vole population density by habitat (Table 3). Voles were the most frequent prey item of coyotes and coyotes hunted more often in habitats with higher vole densities. Litvaitis and Shaw (1980) also found that the habitats most commonly used by coyotes had the highest rodent densities. Todd *et al.* (1981) found that coyotes switched from hunting in forested habitats during years of high snowshoe hare (*Lepus americanus*) populations to open habitats during years of low snowshoe hare populations when mice were consumed most often. Snow tracking has also shown coyotes to disproportionately use some habitats over others (Ozoga and Harger 1966, Hilton and Richens 1975) and it was suggested that this was the result of higher densities of major prey species in those habitats.

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Introduction to the Special Northwest Science Issue The George Fahnestock Memorial Fire Symposium

The papers in this special issue of *Northwest Science* resulted from the George Fahnestock Memorial Fire Science Symposium held in March, 1990, at the Northwest Scientific Association Annual Meeting in Corvallis, Oregon. George Fahnestock was a leader in wildland fire research, and a tribute to his accomplishments and contributions was published last year in *Northwest Science* (Vol. 63, No. 1). The symposium addressed a wide variety of current fire issues. A majority of the papers were submitted for publication in this special issue, but all of them are mentioned to provide proper context for the symposium.

Fire has been a dominant ecological process in Northwestern ecosystems for millennia. Land managers have realized that attempts to totally strangle fire from the landscape are futile, and in fact, usually result in declines in resource values and increased fire control problems. Concurrently, land managers have recognized that the use of fire may contribute to the achievement of land management goals. A paper by Stephen Arno and James Brown (not included in this issue) addressed the strategies available to managers on lands managed for different values—nature reserves, the urban-wildland interface, and a large set of multiple-use wildlands. The use of fire, including prescribed ignitions and prescribed natural fire, together with fire control, complement each other in an integrated fire management strategy.

Decisions about the need to burn depend on management objectives, ecosystem characteristics, and an evaluation of the costs and benefits of burning. "To burn or not to burn" has been a resources management version of Shakespearean drama since the 1920's. The use of fire has been debated from the driest of rangelands to the wettest temperate conifer forests. Evaluation of windstorm-created "blowdown fuels" by Christiansen and Pickford suggest that fuel treatment (such as salvage logging or slash burning) may not be necessary as fuel hazards decline rapidly after such events in the moist Douglas-fir forests of northern Oregon. Omi and Kalabokidis show that the 1988 Yellowstone fires had more severe tree mortality effects in the undisturbed fuels of mature lodgepole pine forests than in areas dominated by young trees where prior timber salvage for bark beetle mortality had occurred. What we consider "natural" disturbance from wind or fire may, from a fuels management standpoint, be acceptable or not depending on the disturbance, the unique climate and biota of the ecosystem, and the management context in which it occurs.

When burning is done in natural or manipulated landscapes, off-site factors are becoming critical decision criteria. The major offsite effect, under most conditions, is air pollution, and slash burn management has focused on reducing smoke during burns. Hall's paper reports on experiments using mass ignition as a means of rapidly consuming fine fuels while preventing large fuels from smoldering.

One of the largest sources of air pollution originates from smoldering combustion of duff, that partially decomposed organic horizon beneath the surface leaf litter. Duff consumption may also create lethal temperatures at the soil surface, killing fine roots, mycorrhizal fungi, and the cambial tissues of trees and shrubs. Frandsen's laboratory experiments are helping to develop a general physical model of duff consumption. The duff burning experiments of Martin and Scott (not included in this issue) provided field data that will empirically support such a model.

Decades of fire suppression have resulted in ecological changes in rangeland and forest ecosystems: altered structure, different species composition, and higher fuel loads. A paper by R. F. Miller (not included in this issue) documented the

landscape changes in eastern Oregon, in particular the dramatic invasion of western juniper into bunchgrass prairie previously maintained by frequent burning. The paper by Sapsis and Kauffman summarizes the initial effects of reintroducing fire into these juniper and sagebrush dominated rangelands, and emphasizes the importance of fire characteristics in different seasons in predicting fire effects.

Many plants have evolved special adaptations to survive the fire regime characteristic of their environment. The paper of Kauffman and Martin, separately submitted to the journal but included in this issue, reports how heat and stratification influence shrub seed germination.

The "ancient forest" preservation controversy in the Pacific Northwest has to date overlooked the importance of past fire disturbance in creating and maintaining old growth forest characteristics. A paper by Andrew Gray (not included in this issue) evaluated the effects of single and multiple burns on the age spans of Douglas-fir regeneration in southern Washington. Such research will help us to explain the very long regeneration lags found in some Douglas-fir forests following historical burns. Agee's paper on Douglas-fir forests of the Siskiyou Mountains shows that these drier forests have experienced multiple fires during their development to old-growth conditions. This frequent fire return interval is in striking contrast to more moist Douglas-fir forests of the Olympic Peninsula and the Cascade Range, with much longer fire return intervals and stand replacement fires.

Humans have had a long and complex association with fire. Our ability to deal with wildland fire is limited by our cultural biases, lack of knowledge of the ecological role of fire in ecosystems, myriad management objectives, and the difficulties of controlling and using fire. Fire is an inextricable component of Northwestern wildlands. Research in basic and applied aspects of wildland fire, as illustrated by this special issue of *Northwest Science*, is essential if our society is to successfully coexist with these inevitable flames in our wildlands.

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Natural Abatement of Fire Hazard in Douglas-fir Blowdown and Thinning Fuelbeds

Abstract

Chronosequences of fuelbeds resulting from precommercial thinning and blowdown in Douglas-fir were measured using standard fuel inventory techniques. Non-linear least squares regressions were fitted to the resulting data. Results confirmed that precommercial thinning slash loses half its original loading and depth within two years. By comparison with published results, the same change in similar fuelbeds in ponderosa pine takes 15 years. Foliage retention on twigs and branches was nil after one year compared to ponderosa pine which retained fifty percent or more of its foliage for at least three years.

Changes in blowdown fuels mirror those in slash, except that more material is present initially. Fine fuels (less than three inches in diameter) fall to background levels within two to four years. Large fuels persist longer and decay more slowly but eventually melt away.

Sound logs become rotten after about 80 years. Findings of this study corroborate similar findings by others, namely that fire hazard in precommercial thinning slash is satisfactorily abated after three years; abatement is similar in blowdown but fuel depth and large fuel loadings decrease more slowly.

Introduction

Forest managers consider the slash left on-site following pre-commercial thinning and other harvesting operations a potential fire hazard. Likewise, these managers perceive that blowdown Douglas-fir (*Pseudotsuga menziesii*) stands constitute a similar but longer-lasting fire hazard. They do not, however, know how long this hazard persists. If they did, they could make more cost effective decisions concerning slash treatment, hazard assessment prior to harvest, fire behavior modelling and land management planning.

The objectives of this study were to develop estimates of the changes over time in fuelbed loading and depth in precommercially thinned and blown down low elevation Douglas-fir stands. The results provide estimates of the duration and decay of physical fuelbed characteristics in stands of this important commercial species. Because fuelbed characteristics strongly affect fire hazard, the results can be used to evaluate the changes in fire hazard over time.

Changes in fuelbed characteristics over time in thinning slash or blowdown can be examined either by series of periodic examinations of one area, or by studying a chronosequence of several areas. Ideally, one would establish permanent plots in a series of units, and return year after year to these same plots to gather fuelbed data and compute rates of decomposition. However, where time is limited, only the chronosequence method is practical. In this method, fuelbeds created at various times in the past are inventoried more or less simultaneously, and the results are interpreted as if the same unit was inventoried in successive years. Carlton (1980) used a similar approach to estimate changes in fuelbeds of ponderosa pine slash.

Much literature on precommercial thinning in Douglas-fir exists, but relatively few workers have explored precommercial thinning as a source of slash, and its expected duration as a fire hazard. Reukema (1964) in a study of litter fall in a young Douglas-fir stand concluded that litter fall in stands is proportional to basal area. Thinning, by removing a portion of the existing basal area, reduced litter fall.

Lawson (1978) studied thinning slash in coastal Douglas-fir in British Columbia. He observed that the falling of needles from their twigs after one winter reduces the expected fire spread almost in half. He concluded that the fire hazard in a thinned stand would, after three years, probably be satisfactorily abated for most situations of risk, weather severity, and fire suppression capability.

Fahnestock (1968) explored thinning slash in ponderosa pine in order to determine how fire behavior in the slash would change over time. He found that by thinning well-stocked stands of pine to a 3.7 by 3.7 m or wider spacing produces a

fuel complex that rates high in rate of spread for at least five years after cutting, and it would burn with a relatively high intensity. Thus, in pine, thinning seriously increases fire hazard for about five years, but in the long run precommercial thinning greatly reduces the vulnerability of stands to fire.

Carlton (1980) studied a chronosequence in ponderosa pine precommercial thinning slash and found that fuel loading took 15 years to decrease by half, and that slash retained half its needles for at least three years.

Fahnestock (1960) studied the flammability of the logging slash of various species. He noted that Douglas-fir usually loses its foliage the first winter after cutting, but exceptions do occur. Fallen needles sometimes form noticeable concentrations on the ground, especially when supported by twigs. Twigs and branches lie increasingly flat with age. Bark disintegration is noticeable at the end of two to three years, but had not progressed far. He concluded that because slash loses most of its foliage in the first year following cutting, the flammability declines very slowly after the first year and is of little consequence by the end of the third year.

After five years, 75 percent of the twigs were retained in their original state, while the foliage lay in dense mats, bound together with fungal mycelia (Fahnestock and Dieterich 1962). Much of the bark on the residue was loose. The fuelbeds examined occupied 79 percent of their original volume and the rate of spread of fire in the fuels studied had declined by 82 percent.

Olson and Fahnestock summarized slash deterioration (1955). For various species in locations from the northern tip of Idaho to the Clearwater River they observed that: fuelbeds compact about 20 to 36 percent during the first year, depending on whether they were lopped; this compaction hastens decay and reduces flammability; Douglas-fir slash loses all its needles after the first year; and finally that the finest fuels (needles and fine twigs) disappear after three years, but larger branchwood persists until brought into contact with the ground.

In summary, previous studies suggest that fine hazard resulting from precommercial thinning in Douglas-fir decreases significantly in two to three years. No quantitative descriptions of such fuels have been given, nor have studies of fuelbeds resulting from blowdown been reported. Quantitative measures of both types of fuels are necessary if fire hazard is to be evaluated using currently available models.

Methods

This study was conducted in the Bull Run Watershed, thirty miles northeast of Portland, Oregon. Elevation in the area varies from 230 m to 1250 m. Yearly precipitation in the area averages between 230 and 430 cm with most falling in the winter months. The area typically experiences a summer drought period during July and August.

Two sets of sampling sites were used. One set of fourteen areas had been precommercially thinned. The ages of thinning in this set ranged from zero years (thinned during the summer of 1987) to fifteen years (thinned during the summer of 1972). The second set of sites were four areas that had stands of large trees which had blown down at various times. Stands containing blowdown were found after extensive field reconnaissance, review of aerial photographs and maps, and personal interviews with local personnel. Age since blowdown ranged from four years (blown down in 1983) to eighty-one years (blown down in 1906). Blowdown ages were determined from U.S. Forest Service and City of Portland records for the area.

The selected precommercial thinning units were stocked primarily with Douglas-fir. Minor amounts of western hemlock and western redcedar were also encountered. Units selected showed relatively homogeneous expanses of untreated slash. Areas adjacent to roads that had been chipped were not sampled.

Twenty-four plots were systematically located within each unit in grid fashion. Plot centers were generally established 60 m apart, but were sometimes as little as 30 or as much as 140 m apart.

Two 7.6 m long transects were laid out perpendicular to each other at the plot center. The first was in the direction of main travel between plot centers. The second was at right angles to the first.

Duff depths were measured at 0.3 and 1.8 m from plot center. The high particle height was measured at 90, 120 and 150 cm from the plot center along each transect. The high log height (measured from ground to the top of the log or stem) was measured at 1.5, 3, 4.5, 6, and 7.5 m points on the transect. If foliage remained on any twig intersecting the transect, it was tallied. Generally, foliage intercepts were counted from zero to 7.3 m. However, if a large number of

intersections were to be counted, then the length of the transect was shortened to 60 cm to facilitate tallying.

The fuel particle intercepts along the transect were counted into five diameter classes: 0 to 0.6 cm; 0.6 to 2.54 cm; 2.54 to 7.6 cm; and particles larger than 7.6 cm, sound or rotten particles counted separately. Particles in the 0 to 0.6 cm class were counted along the first meter of the transect. The intercepts for particles in the 2.54 to 7.62 cm class were counted along the first two meters of the transect, and intercepts for both sound and rotten material larger than 7.62 cm in diameter were measured along the transect out to 7.3 m. Logs and large limbs were counted as rotten if they "gave" or broke apart when kicked.

The fuel loading for each class was estimated by the arithmetic mean of the twenty-four plot estimates, for each of the units of that particular age that were sampled. Formulas for converting particle intercept counts to weight per unit area were taken from Brown (1974).

Similarly, in the blowdown fuelbed, the average loading by size class was computed by using the arithmetic mean of the plot estimates for each unit of a particular age that was sampled.

The average duff depth in both the thinning and blowdown slash was the arithmetic mean of the two depths taken along each transect. The average high particle intercept for both types of slash was the arithmetic mean of the three intercepts measured along each transect, and the average high log intercept for both types of slash was the arithmetic mean of the five intercepts measured along each transect.

Characteristics of Thinning and Blowdown Slash Fuelbeds

The ranges of data from the thinning slash units are given in Table 1. Ranges of data from the blowdown units are given in Table 2. A variety of regression models have been suggested in the literature on deterioration and decay of slash materials. Several such models and variants of them were applied to the data from this study. Because the agency that funded this study required the results to be given in English units, the regression statistics are so reported in the following tables. Tables 3 and 5 report the regression statistics for fuelbed loading for precommercial thinning slash and blowdown fuelbeds, respectively. Tables 4 and 6 report the corresponding statistics for fuelbed depth. Figures 1 through 6 show the trend lines for these equations. The axis labelling in these figures has been transformed to reflect the data in metric units.

TABLE 1. Thinning Slash Fuelbed Data Ranges

		Minimum	Maximum
0-0.6 cm	(tonne/ha)	0.61	5.78
6-2.54 cm	"	1.21	8.51
2.54-7.6 cm	"	0.67	24.66
>7.6 cm sound	"	0.00	8.06
>7.6 cm rotten	"	0.00	2.29
Total fuel loading		4.20	46.97
Duff depth	(cm)	0.31	2.81
High particle height	"	7.36	67.84
High log height	"	1.64	26.02
Basal area removed	(sq. m/ha)	0.89	15.39

TABLE 2. Blowdown Fuelbed Data Ranges

		Minimum	Maximum
0-0.6 cm	(tonne/ha)	.79	2.25
0.6-2.54 cm	"	3.65	5.12
2.54-7.6 cm	"	4.31	16.62
>7.6 cm sound	"	6.35	583.6
>7.6 cm rotten	"	47.51	294.8
Total fuel loading	"	194.1	734.4
Duff depth	(cm)	51.3	29.0
High particle height	"	134.9	1620.0
High log height	"	169.9	727.5

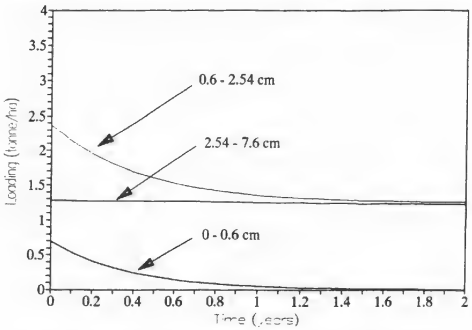

Figure 1. Trend line of plot averages for fine fuel loading in precommercial thinning slash fuelbeds, Bull Run study area, Oregon.

Fine fuel loading in precommercial thinning slash decreases with time since thinning. The initial rate of change is high, as one would expect, and approaches a steady-state value within a short time (Figure 1).

TABLE 3. Regression statistics from fuels inventory on precommercial thinning slash plots. Equation form is *Loading = a + EXP(b * Years).*

Diameter Class (mm)	Parameters		MSE	*t*-value		Standard Error	
	a	b		a	b	a	b
0-0.6 cm	0.6210	−2.6462	0.511	2.77	0.39	0.22	6.76
0.6-2.54 cm	1.1072	−2.2958	1.148	3.24	0.32	0.34	7.20
2.54-7.6 cm	1.1418	−0.0228	7.947	1.15	0.10	0.99	0.22
>7.6 cm sound	0.1012	−0.0277	1.192	0.26	0.30	0.39	0.09
Equation: *Loading* = a + b * Time							
>7.6 cm rotten	−0.059	0.0424	0.177	0.99	4.33	0.06	0.01

Note: values based on 12 degrees of freedom.

TABLE 4. Regression statistics from fuels inventory on precommercial thinning slash plots, fuelbed depth. Equation form for duff is *Depth = a + EXP(b * Time).* Equation form for high particle and high log fuelbed depths is *Depth = a * EXP(b * Time).*

Depth Measure (in)	Parameter		MSE	Standard Error	
	a	b		a	b
Duff	−0.362	0.027	0.064	0.081	0.009
High Particle	16.9	−0.56	48.8	2.567	0.039
High Log	8.01	−0.08	8.48	1.168	0.051

Note: values based on 12 degrees of freedom.

TABLE 5. Regression statistics for fuelbed inventory on blowdown slash plots. The equation form is *Loading = a + EXP(b * Years),* except for the >7.62 cm sound class, which is *Loading = a * EXP(b * years).*

Diameter Class (mm)	Parameter		MSE	*t*-value		Standard Error	
	a	b		a	b	a	b
0-0.6 cm	−0.258	−0.0008	0.21	1.17	0.13	0.20	0.01
0.6-2.54 cm	0.626	−0.0047	0.22	2.88	0.54	0.22	0.01
2.54-7.62 cm	3.312	0.0396	3.45	1.34	0.08	2.47	0.52
>7.62 cm							
sound	146.9	−0.0551	0.73	15.4	5.89	0.32	0.01
rotten	35.90	−0.0568	328	5.14	23.3	6.99	0.01

Note: values based on 12 degrees of freedom.

TABLE 6. Regression statistics from fuels inventory on blowdown slash plots, fuelbed depth. Equation form for high particle and high log fuelbed depths is *Depth = a * EXP(b * Time).*

Depth Measure (in)	Parameter		MSE	Standard Error	
	a	b		a	b
High Particle	24.05	−0.0157	0.64	0.28	0.01
High Log	19.49	−0.0127	0.41	0.18	0.01

Note: values based on 12 degrees of freedom.

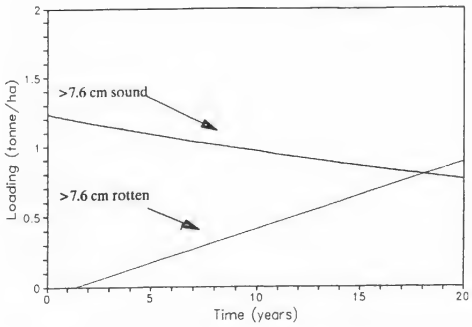

Figure 2. Trend line of plot averages for large fuel loading in precommercial thinning slash fuelbeds, Bull Run study area, Oregon.

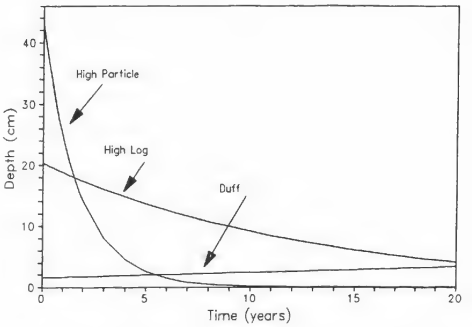

Figure 3. Trend line of plot averages for fuelbed depth in precommercial thinning slash, Bull Run study area, Oregon.

Fuels in the >7.6 cm rotten category were uniformly sparse over all units surveyed (Figure 2). Only four of fourteen units had any fuels in this category at all, and these were in older units. Thus, trends for this size class may be questionable. But overall, the trends for fuel loading in all size classes of precommercial thinning slash seem reasonable.

Needle persistence in precommercial thinning slash was measured as the number of twigs counted along sampling intercepts which retained at least three needles per meter of transect. For current season slash, needle persistence averaged 13 twigs per meter; for 1-yr old slash, it averaged 0.53 twigs per meter. No needles were observed in slash older than 1 year. For all practical purposes, needle loading can be assumed to fall to zero by the start of the second season after thinning.

Duff depth increases gradually over time, as one would expect (Figure 3). Because the data range stops at 15 years, the flattening of the duff accumulation curve observed repeatedly in biomass studies is not represented by this model. Had the data included older sites, this flattening would no doubt have been included.

Both the high particle and high log heights decrease over time, with greatest rate of change early on, again as one would expect (Figure 3). The high particle height drops much more quickly than the high log height. Fuelbed depth, as measured by high particle height, falls to fifty percent of its original value in less than two years. By contrast, depth as measured by high log height does not decrease to fifty percent of the original depth for nearly nine years. This probably reflects the rapid breakage of the twigs and small branches supporting the thinned stems in the first few seasons after thinning, and the much slower process of stem decay and failure of the larger branches which support the heavier thinned stems.

Figures 4 and 5 show the changes in fuelbed loading in blowdown fuels. In these models, the trends of loading over time for the fine fuels (0-0.6 cm through 2.54-7.6 cm classes) do not fall off as rapidly as those for precommercial thinning slash, probably because fine materials in these species on the west slope of the Cascades decay rapidly and are essentially gone from the surface litter within three years. Since the first data point for the blowdown chronosequence was four years since the disturbance event, the period of most rapid decay had already passed, and is therefore not reflected in the resulting models.

The large material (>7.6 cm sound and >7.6 cm rotten) behaves as one would expect within the range of the data. Loading of sound material larger than 7.6 cm starts high and decreases to a low value. Loading for rotten material larger than 7.6 cm starts low and stays low for nearly 50 years, then begins to increase. At the limit of the data range, this increase nearly accounts for the entire loss of sound material in the >7.6 cm size class.

Fuelbed depth as measured both by high particle height and high log height gradually decreases (Figure 6). Initially, depth as measured by high particle height exceeds that measured by high log height by about 12.7 cm. At the limit of the data (81 years), the two measures of fuelbed depth converge. This reflects what typically happens; as time passes even the largest branches decay and fall, leaving the logs themselves as the highest particles in the original fuelbed.

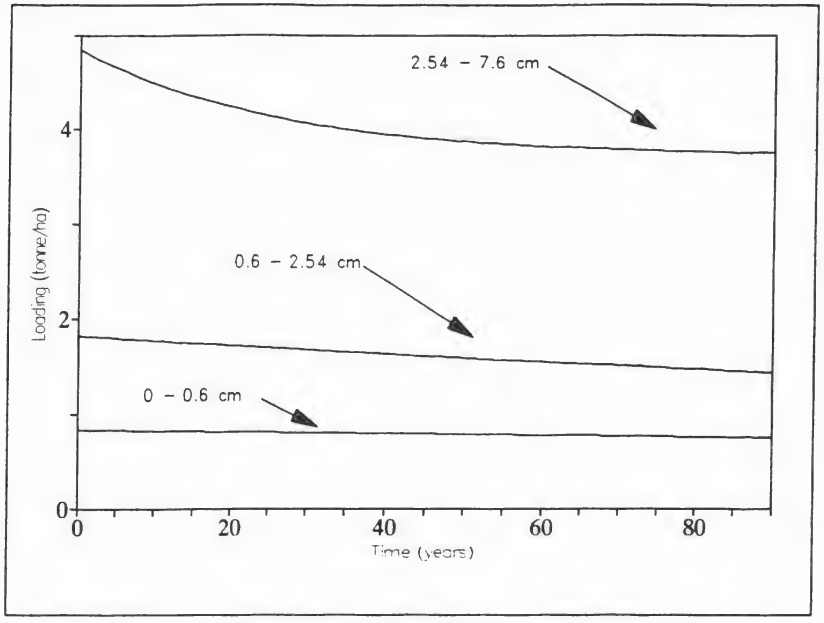

Figure 4. Trend line of plot averages for fine fuel loading in blowdown fuelbeds, Rull Run study area, Oregon.

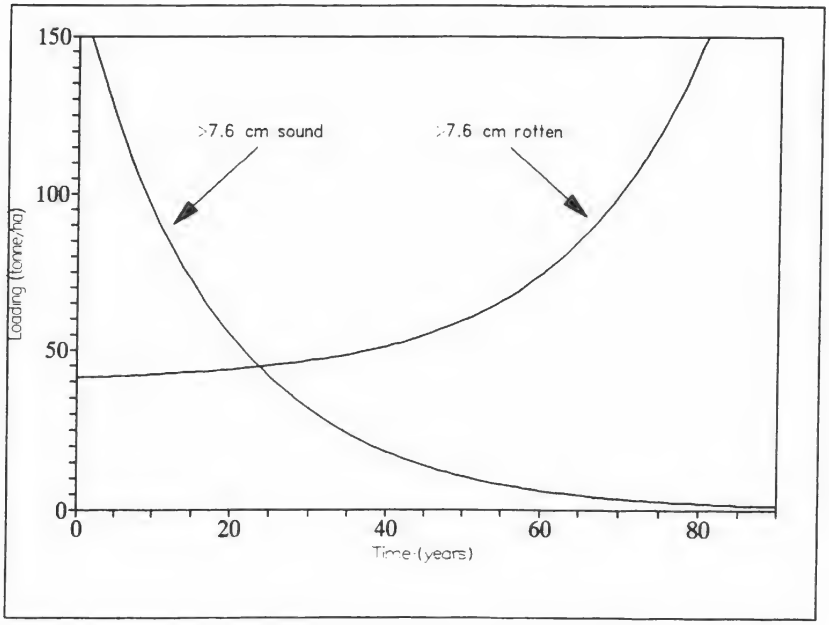

Figure 5. Trend line of plot averages for large fuel loading in blowdown fuelbeds, Bull Run study area, Oregon.

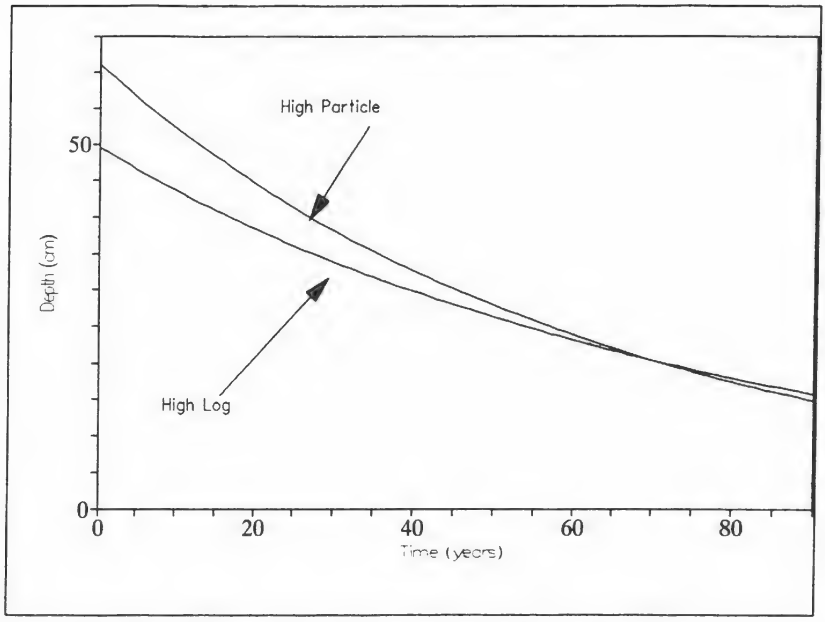

Figure 6. Trend line of plot averages for fuelbed depth in blowdown fuelbeds, Bull Run study area, Oregon.

The variation in duff depth with time since disturbance showed no consistent or logical pattern. Numerous studies have shown that transfer rates of material into and out of the duff layer depend on more than just time, and so no attempts to develop relationships for duff depth were made.

Discussion

The results of this study should be generally applicable to the western slope of the Cascade Mountains from about Mt. Jefferson to Mt. Rainier, and the western Olympic Peninsula. These areas are similar in rainfall and climatic patterns to the Bull Run, and thus should exhibit similar trends in decay. The results may also be applicable to the Oregon Coast Range and southern Oregon Cascades as well, but should be applied with caution, and with provision for testing predictions against rates of fuelbed decay.

Fuelbed changes in west-slope precommercial thinning slash are much more rapid than in east-slope ponderosa pine thinning slash (Carlton 1980). Fuelbed loading of fine fuels decreased by half in less than two years in the study area, while ponderosa pine fuelbeds lost less than half their loading over a period of 15 years. The time required to lose half the fuel loading in this study is more rapid by a year than that observed by Olson and Fahnestock (1955) in northern Idaho. Foliage on slash in this study disappeared within a year, while ponderosa pine slash lost only 50 percent of its needle mass in 3 years. This rate of needle loss agrees with that observed by Fahnestock (1960) in his study of the flammability of logging slash.

Fuelbed depth, measured by high particle intercept, dropped to 50 percent of the original value in less than two years in the thinning slash in this study, while a corresponding change took 10 years in ponderosa pine. This study substantially corroborates Lawson's finding (1978) that fire hazard in precommercial thinning slash is satisfactorily abated after three years for most situations of risk, weather severity and fire suppression capability.

Fuelbed changes in fine fuels in blowdown situations reflect patterns of change similar to those in precommercial thinning slash, except that there is typically more materials to begin with. Fine fuels essentially fall to background levels in two to four years. Larger (2.54-7.6 cm diameter) branch materials and 1000-hr fuels persist for longer

periods and decay more slowly, but eventually 'melt' away. This agrees with observations of fire-killed timber by Kimmey (1955), in California, and Basham (1957), in Ontario. Forest managers fear the contribution of blowdown logs to fire hazard. This study suggests that the conversion of sound 1000-hr fuels to rotten 1000-hr fuels is a gradual process that nears completion in about 80 years under conditions like those found in the Bull Run study area.

The results of this study should enhance the quality of decisions regarding treatment and abatement alternatives in silvicultural slash and blowdown areas in the Northwest. However, as with any study of limited scope, the results should be applied with caution, and with provision for continued testing against observed conditions.

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Fire Damage on Extensively vs. Intensively Managed Forest Stands Within the North Fork Fire, 1988[1]

Abstract

The Greater Yellowstone fires of 1988 provide an opportunity to study important distinctions between lands managed for preservation versus multiple uses. We surveyed fuel loadings, fire severity, and fire damage in extensively managed, mature forests and in intensively managed, clearcut reproduction areas. Unburned, mature forests support higher fuel loadings in the large and small woody fuel size classes. Fifty percent of the 50 fire severity estimates in mature forest plots were given the highest ratings possible for flame length and ground char. Fire damage was rated highest on 89% of the 55 mature forest plots, based primarily on crown scorch indicators. By contrast, highest fire damage ratings were associated with only 20% of the 45 regeneration sites surveyed. Fire severity and damage were moderated in intensively managed areas. Intensively managed forest areas improve fire management options in the Greater Yellowstone Area.

Introduction

The Greater Yellowstone fires of 1988 provide an opportunity to focus on important distinctions between lands managed for preservation versus multiple uses. Historically, within Yellowstone National Park (YNP), the preservation mandate had allowed no active fuels management prior to 1988. By contrast, on the adjacent Targhee National Forest (TNF), fuels have been actively manipulated since 1960 in conjunction with multiple use objectives, primarily timber management.

The North Fork Fire was started by woodcutters on the Moose Creek Plateau of the TNF on 22 July 1988. Fueled by strong SW winds, the fire quickly spread into YNP. Throughout the next 7 weeks (including eventual merger with the Wolf Lake Fire), the North Fork Fire burned over 200,000 ha of national park, national forest, and Idaho state lands. Numerous developments were threatened, including Old Faithful Village, Madison Junction, Norris, Canyon Village, Mammoth Hot Springs, and Tower-Roosevelt. The communities of West Yellowstone and Gardiner also were endangered. On two separate occasions (27 August and 2-3 September), wind shifts blew the fire back onto the TNF, with estimates ranging from approximately 4,500 to 7,000 ha of national forest burned area (Greater Yellowstone Coordinating Committee 1989, Hardin 1988, respectively). The fire was finally declared controlled in early November, 1988, after the area received significant moisture from snowfall.

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This paper presents a survey comparison of fuels, fire severity, and fire damage in forested stands on national park and national forest lands. For purposes of this paper, we define mature forest sites on national park and national forest lands as *extensively managed;* we designated sites on the TNF with reproduction after clearcutting as *intensively managed.* Based on these distinctions, we draw comparisons between fire severity and damage in extensively and intensively managed forest lands within the vicinity of the Moose Creek Plateau. We conclude with inferences about fire potential on lands managed for preservation and the importance of intensive management at the boundary.

Study Area and Objectives

The Targhee National Forest borders the southwestern boundary of Yellowstone National Park in Idaho (Figure 1). The 57,000 ha Moose Creek Plateau abuts the national park in Idaho, south of the Montana state line. Aside from timber harvesting, other uses identified in the TNF Plan (USDA Forest Service 1985) include roaded recreation, wildlife (elk and grizzly habitat), and grazing. Elevations in the study area range from 2,000 m on the plateau to 2,500 m along the YNP boundary. The dense lodgepole pine (*Pinus contorta*) stands in the area have been salvage-logged in response to mortality from mountain pine beetle (*Dendroctonus ponderosae*) infestations since 1960. The widespread infestation also affected trees on adjacent national park lands.

We restricted our investigation to the point of origin (about 50 m from the YNP boundary), the initial area burned on national forest and national

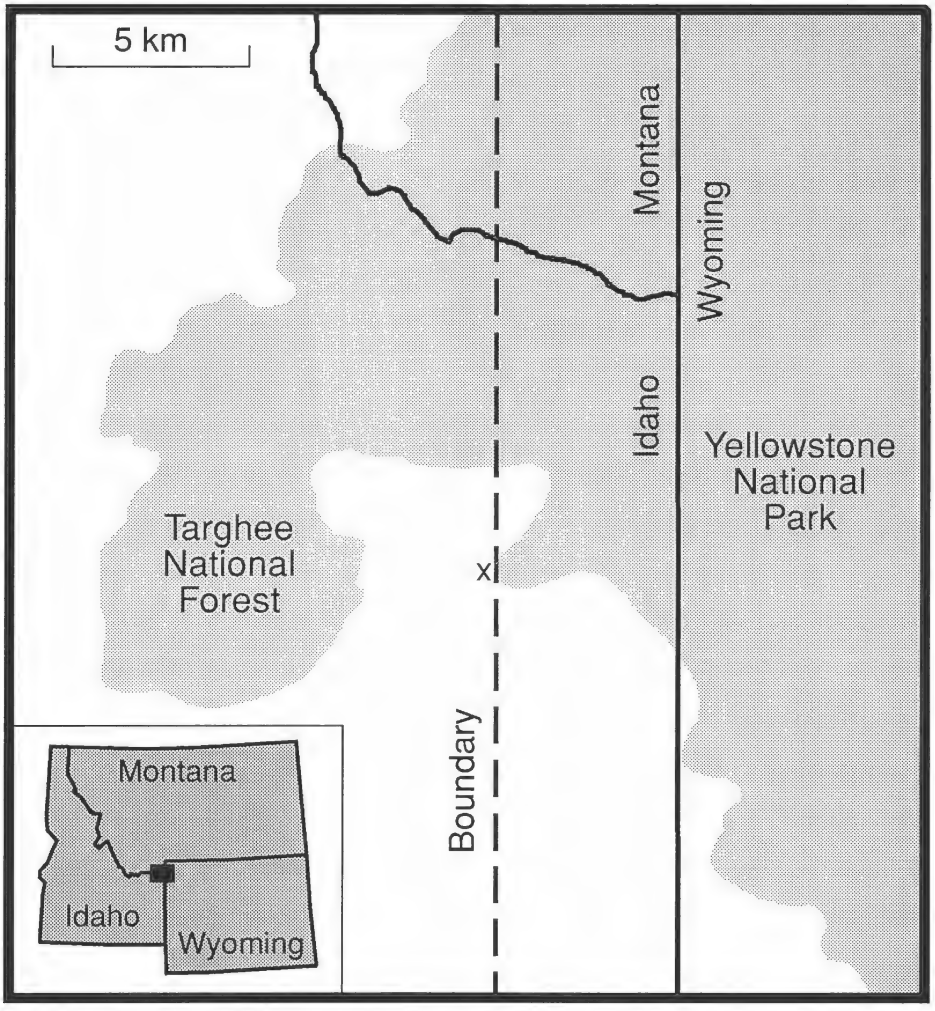

Figure 1. Silhouette of portions of the 1988 North Fork Fire and study area. The fire originated on the Targhee National Forest in Idaho (x = point of origin), on 22 July 1988, and spread quickly into Yellowstone National Park. Shifting winds blew the fire back onto national forest land over one month later, north of the point of origin.

park land (8 ha and 140 ha respectively), and the two subsequent wind-driven burns onto the national forest. Based on initial examination of fire documents and maps, we decided to focus on distinctions between extensively managed versus intensively managed forest stands in the vicinity of the Moose Creek Plateau.

Approximately 54 percent of lands within the North Fork burn on the Moose Creek Plateau were mature (Hardin 1988). These consisted of standing timber between alternate clearcut strips, and areas yet to be entered for timber harvest. By contrast, 100 percent of national park lands were mature, due to the National Park Service (NPS) preservation philosophy.

Our objectives were:

1. to compare fuels in mature, extensively managed forests versus intensively managed areas (naturally regenerated following cutting);
2. to estimate fire severity (defined below) in extensively managed areas;

3. to assess fire damage (defined below) in extensively versus intensively managed areas.

Methods

We delineated two vegetative condition classes of primary interest for our study, based on preliminary discussions with TNF personnel (pers. comm. with Mr. Don Black, district fire management officer, 1988). Stands were delineated as either extensively managed (on national park and national forest land) or intensively managed, as follows:

- *Extensively managed stands:* Mature to overmature, dominated by lodgepole pine overstory, associated with various tree species, depending on elevation. At lower elevations, associated species include scattered mature Douglas-fir (*Pseudotsuga menziesii*) and small aspen clones (*Populus tremuloides*). At higher elevations, associates include subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), limber pine (*Pinus flexilis*), and whitebark pine (*Pinus albicaulis*). Principal understory shrubs include grouse whortleberry (*Vaccinium scoparium*) and blue huckleberry (*V. globulare*). Pre-fire mortality from the pine beetle ranged to as high as 70% in many stands.

- *Intensively managed stands:* Clearcut national forest areas, mostly regenerated naturally following timber harvest and slash disposal, consisting of lodgepole pine seedlings and saplings (< 20 years old). Scattered individual Douglas-fir, subalpine fir, and aspen occur. Stocking densities are as high as 15,000 trees/ha in the older reproduction, with tree heights from 0.9-5.0 m. Younger lodgepole pine reproduction (< 8 years old) areas consist of smaller trees (0.3-0.9 m height) and lower stocking density (2,000-7,500 trees/ha). On harsher sites, pinegrass (*Calamagrostis rubescens*) and elk sedge (*Carex geyeri*) occur frequently.

Detailed information on the structure of burned and unburned stands was not collected. Two primary habitat types (Steele *et al.* 1983) are descriptive of the burned area. Ninety percent of the area is occupied by the *Abies lasiocarpa/Vaccinium scoparium* (ABLA/VASC) habitat type; *Abies lasiocarpa/Vaccinium globulare* (ABLA/VAGL) occupies the remainder (Hardin 1988).

We surveyed the North Fork burn area on national forest and national park land during July, 1989. We restricted our focus to burned and unburned plots as defined above. On national forest land, we had difficulty locating unburned mature stands within the burn area; in fact, less than 4% TNF burned area consisted of mature, extensively managed stands (Hardin 1988). Eventually, ten unburned mature forest stands were located outside the burn perimeter and in unburned islands within the fire perimeter (five each on either side of the TNF-YNP boundary).

Our intent was to distinguish between fuels, fire severity (Ryan and Noste 1985), and fire damage in extensively vs. intensively managed forest stands within the study area. Fuel inventory transects (after Brown 1974, and Burgan and Rothermel 1984) were randomly located in each of the ten unburned mature forest stands. Each unburned stand was assumed representative of the fuel profile which existed prior to the fire. In the adjacent burned stand we completed a fire severity transect (randomly located), consisting of five 30x60 cm subplots at 3 m intervals. Independent estimates were recorded for fire intensity (which relates to heat pulse received by above-ground vegetation, in the subplot vicinity) and depth of char (heat pulse directed to the duff and soil within the subplot), for a total of 50 fire severity estimates (10 transects times 5 estimates per transect). Instead of averaging all intensity and depth of char estimates per transect (after Ryan and Noste 1985), we decided to present the raw data to depict the variability in fire severity within the burned area.

Also, we developed ocular estimates for fire damage in each burned stand, using the following criteria:

Unburned: Fire did not enter the stand;
Light: Surface burn without crown scorch;
Spotty: Irregular crown scorch;
Moderate: Intense burn with complete crown scorch;
Severe: High intensity canopy burn, with crowns totally consumed.

These criteria represent a synthesis of standards (see Wells *et al.* 1979, Ryan and Noste 1985, Weatherspoon and Skinner 1989, and the burned area map *in:* Greater Yellowstone Coordinating Committee 1989), adapted to suit our specific needs. We applied these same criteria for assessing damage to an additional 45 intensively managed sites and adjacent mature stands on national forest lands. (No intensively managed sites exist

on national park land due to NPS policy). A total of 55 different stands was included in our survey.

Results

Fuel Loading

Fuel loadings in mature, extensively managed stands (national park and national forest) are summarized and compared against intensively managed, regenerated areas in Table 1. Generally, the mature forest plots support higher loadings than areas clearcut and cleared, for the large, small, and litter fuel categories. In the large fuel category, loadings for rotten, decaying fuels were significantly higher in mature forests (12.0 vs. 2.9 metric tons/ha). Higher loadings were observed for large sound fuels and duff in mature forests, but differences were not significant due to the high variability in these estimates. Also, fuelbed depth (slash plus litter) was significantly higher in the mature forest plots (7.0 cm versus 2.5 cm).

TABLE 1. Inventoried fuel loadings (metric tons/hectare) for duff, litter, small woody fuel (< 7.6 cm diameter), large woody fuel (> 7.6 cm diameter), dead grasses and shrubs, and live fuels in unburned, extensively managed (mature) stands, versus unburned, intensively managed (regeneration areas), in the vicinity of the Moose Creek Plateau (standard errors parenthesized).

Fuel Component	Extensively Managed Stands (n = 10)	Intensively Managed Areas (n = 10)
Duff[a]	27.7 (7.7)	15.2 (3.9)
Litter[b]	3.1 (0.5)	1.6 (0.2)*
Small Woody[c]	5.1 (1.0)	4.3 (0.7)*
Large Woody[c]	28.8 (8.6)	8.1 (2.0)*
Dead Grasses & Shrubs[b]	0.03 (0.02)	0.02 (0.01)
Live Grasses & Shrubs[b]	0.10 (0.05)	0.07 (0.03)
Live Small Trees[d]	– –	21.1

*Mature forest loading significantly higher than regenerated areas ($p < .10$)

[a]After Brown et al. (1982).

[b]After Burgan and Rothermel (1984).

[c]After Brown (1974).

[d]Point estimate from Brown *et al.* (1982), based on weights for trees of average height and stocking densities (trees/ha) for plantations in the area. Small trees were an insignificant component of mature stands and were not inventoried.

Fire Severity in Mature Forests

Fifty percent of the 50 fire severity estimates in mature forest plots were given the highest ratings possible for flame length and ground char (Figure 2). Of these 25 highest ratings, 15 occurred on national park and 10 on national forest plots. In these plots, overstory trees were killed. Litter and duff were completely consumed over much of the area, along with most twigs and small surface fuels. Evidence for soil discoloration due to soil heat pulse was difficult to detect, given the time (1 year) between the fire and our survey.

On the remainder of mature forest plots (25), fire severity ratings varied from light to moderate (Figure 2). In general, on these plots varying degrees of litter and duff were consumed, but surface twigs and branchwood remained.

Overall, as shown in Figure 2, the entire range of ground char classes was observed in our fire severity estimates. By contrast, flame length classes were either low (classes 1 and 2) or very high (class 5).

Fire Damage in Extensively Managed vs. Intensively Managed Stands

Fire damage ratings in mature, extensive forests versus regeneration areas are compared in Figure 3. Nearly 89% of the 55 extensively managed sites received the highest fire damage ratings (moderate and severe), whereas less than 20% of the 45 intensively managed sites received the same ratings. Over 80% of the intensively managed sites received ratings of "unburned," "light," or "spotty" fire damage.

In each of the 45 regeneration sites surveyed within the burn, we also rated fire damage to the adjacent mature stands (Figure 4). There were 7 cases in which "moderate" or "severe" regeneration damage was accompanied by "severe" damage to the adjacent mature stand. However, in 38 regeneration sites damage was rated "unburned," "light," or "spotty," while damage to the adjacent mature stand was primarily "moderate" or "severe." Thus high fire damage in adjacent extensively managed stands was more often associated with lower levels of fire damage in intensively managed stands (38 of 45 cases).

Discussion

Most of the mature, extensively managed stands within the North Fork burn area had moderate or severe fire damage. By contrast, most of the intensively managed regeneration areas had light or no damage. Although these findings are based on

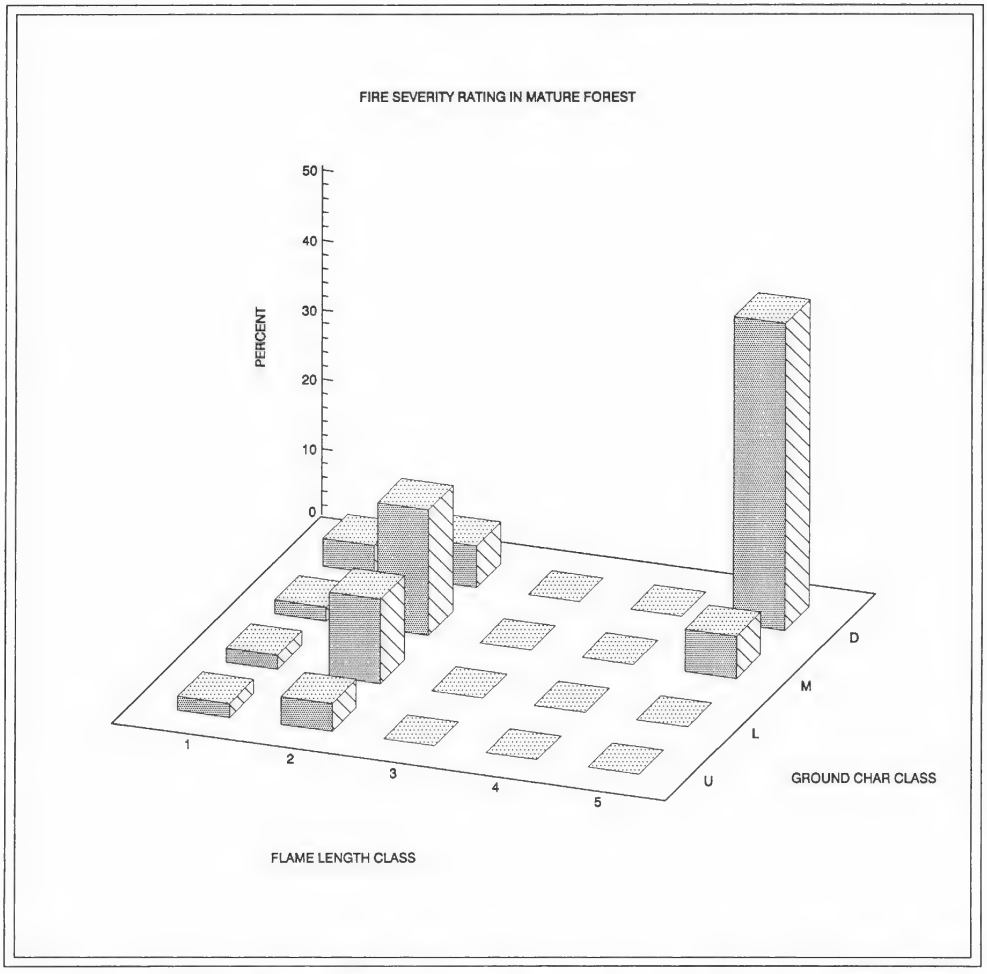

Figure 2. Distribution of 50 fire severity ratings (after Ryan and Noste 1985) recorded in 10 extensively managed, mature forest stands, near the North Fork Fire's origin (Fig. 1). Fifty percent of the estimates were assigned the highest flame length class, 44% with the deepest ground char and 6% with moderate ground char.

a limited field survey, we feel that our results are indicative of significant differences between fire characteristics in extensively versus intensively managed stands. Further, our results are in general agreement with Hardin's (1988) photo survey, which reported that 7% of sawtimber stands and 34% of regenerated stands in the North Fork burn "had escaped fire damage." Reasons for this contrast between mature forest and regenerated stands can be understood in terms of the fuel inventory distinctions.

The higher flammability of extensively managed, mature stands in the study area can, in part, be explained by the higher litter, small fuel loadings (< 7.6 cm), greater large fuel loadings (> 7.6 cm), and higher fuelbed depth as compared to intensively managed areas. Fuelbed and stand differences between mature and immature stands also provide insights into comparative fire effects on lands managed for preservation vs. multiple uses in the Greater Yellowstone Area (GYA).

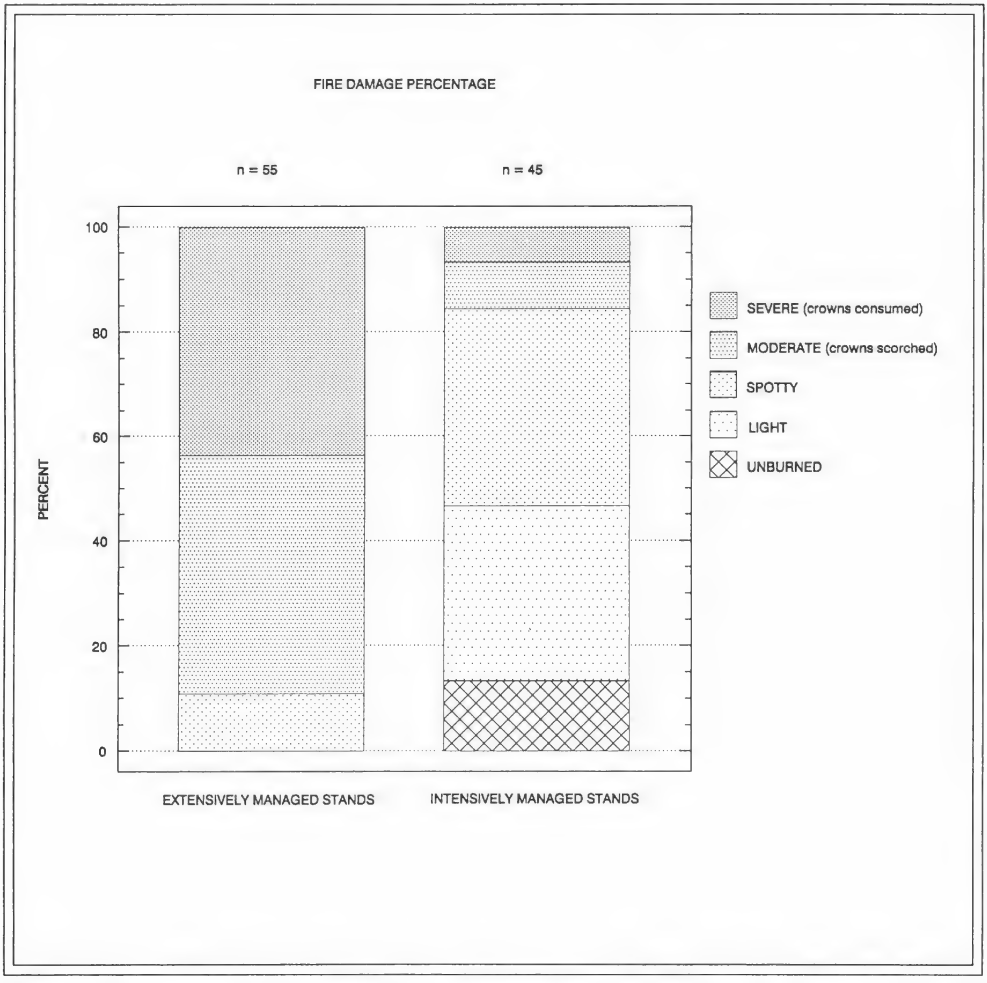

Figure 3. Distribution of fire damage ratings on 55 plots located in extensively managed, mature forest areas (by %), versus ratings on the 45 intensively managed, regeneration sites. Plots were located within the North Fork Fire perimeter, near the point of origin and subsequent burn areas (Fig. 1).

The higher loadings of small fuels and greater fuelbed depths may contribute to higher fire intensities in the mature forests. The higher levels of large fuels also provide a larger heat pulse after flaming, contributing to higher levels of fuel consumption, and greater severity and damage in the mature forest. Usually, large fuels do not contribute greatly to rate of spread and flaming characteristics (Burgan and Rothermel 1984). However, during the extended drought of summer, 1988, lower fuel moistures in large sound and rotten fuels may have increased both fire intensity and depth of charring in the mature forest. Consequently, the mature forest endured greater fire damage than reproduction, even though fire severity was not uniform in extensively managed stands.

We did not observe the fire behavior during the North Fork Fire so we can only speculate about the differences in fire severity in mature forests vs. regeneration areas. In fact, we do not know for sure if fire spread was predominantly from reproduction into the mature forest, or vice versa. However,

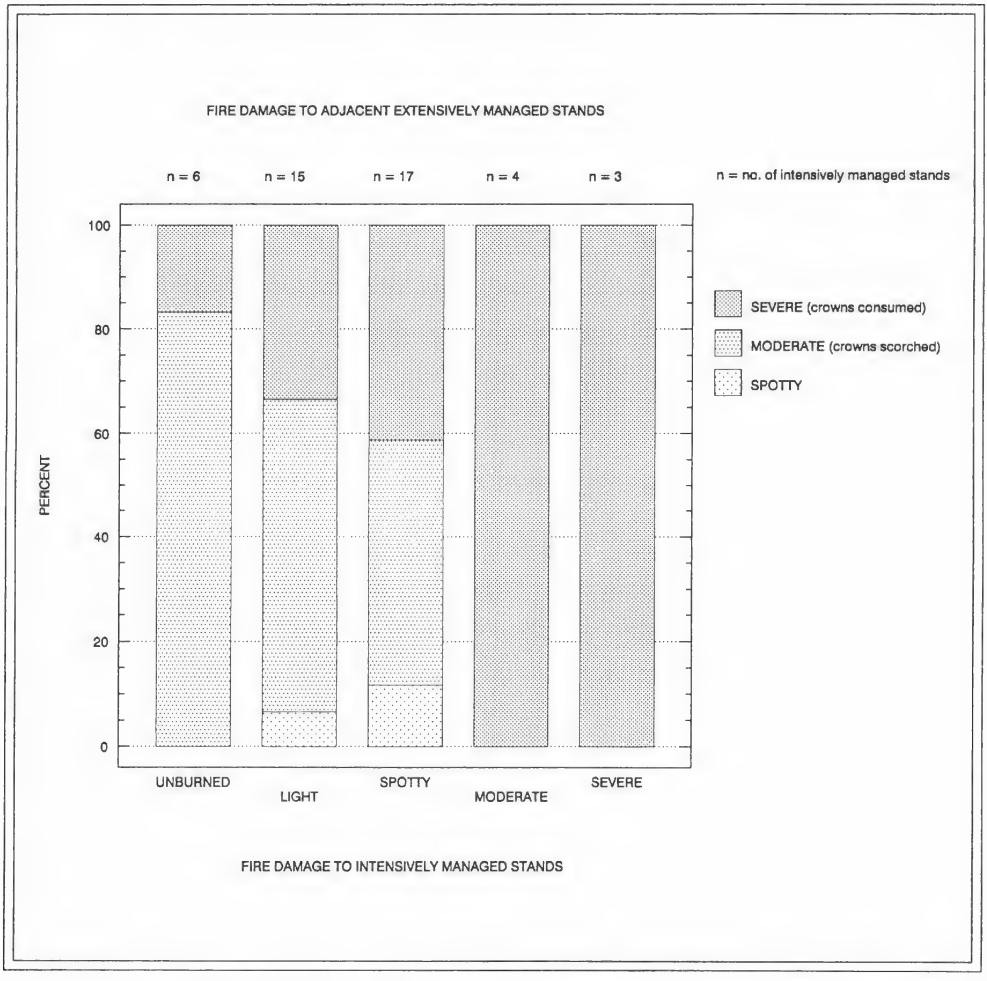

Figure 4. Conditional distribution of fire damage to adjacent extensively managed (mature) forest stands, given damage levels in 45 intensively managed (regenerated) sites. For example, where fire damage to regeneration was light (n = 15) or spotty (n = 17), 93% and 88% (respectively) of adjacent mature stands received moderate or severe damage.

regeneration areas did seem to abate the intensity, severity, and damage. Like Weatherspoon and Skinner (1989), we observed patchy burns in regeneration areas. Although localized damage did occur in regeneration areas, we likewise did not observe a general increase in severity from the edge inward.

We restricted our attention to fuel loading contributions to variations in fire severity and fire damage, although numerous other independent variables might also be important. These include fine fuel continuity (surface and tree crown), elevation, aspect, slope, and crown diameter. In areas subjected to past fuel removal after logging, we also did not have information on time since logging/fuel treatment, fuel treatment method, or intensity of fuel treatment. We also did not account for the higher density of access roads in treated areas, which may have affected fire spread through the area.

Although collection of these data was beyond the scope of our survey investigation, we feel that

the North Fork Fire would have probably burned with greater localized intensity in the absence of fuel management activities. The fuel complex in intensively managed areas is simply less conducive to fire spread than a stand supporting standing and fallen dead trees, killed by the mountain pine beetle. Although natural decomposition would eventually reduce the fire hazard in the infested stand, judicious fuel treatment may be a more attractive alternative, especially in areas where public safety and resource utilization are high priorities.

Conclusions

The 1988 Yellowstone fires illustrated the dramatic contrast between prescribed natural fire strategies on national park and national forest lands. Ironically, high severity wildfires were tolerable under the national park's preservation philosophy; however, high severity fires were considered unacceptable on adjacent national forest lands managed for multiple uses.

Clearly, sound management practices are required if preservation and multiple-use policies are to co-exist in an area. It is not our intent to debate the merits of preservation vs. multiple use management in this paper. However, our data suggest marked distinctions in fuels and flammability between lands managed under these two philosophies. As a result, mature forest stands were more combustible and sustained greater fire damage than adjacent regeneration areas.

The mature forests were more combustible since they consisted of beetle-killed lodgepole pine trees. Timber removal reduced fire damage through disposal of large quantities of standing and fallen dead material. Thus fuels management accomplished through timber removal appeared to reduce fire damage, especially since harvest was followed by removal of residues. Apparently, flammability was lower in intensively managed areas since insufficient time had elapsed since harvest to allow accumulation of surface fuels, or tree mortality by insects and disease. Since environmental conditions (wind and moisture) supported severe fire behavior in adjacent mature stands, the reduction of fuels in intensively managed areas was at least partially responsible for their lower flammability.

While we have focused primarily on fuels and fire characteristics at the Park boundary, our findings could relate to strategies within YNP as well. Within Park boundaries, fuel manipulation should be considered as an option for both unburned and burned areas. In unburned areas fuel hazards will continue to accumulate over time. Concurrently, the amassing snags and decaying materials may provide important habitat for insects, birds, and other wildlife. However, eventually a fire will break out, perhaps under drought conditions similar to 1988, and threaten life and property.

In burned areas, fire-killed trees will eventually fall over and could contribute to high fuel hazards in the future. Reduction of hazardous fuels should be considered especially near high-value resources or in strategic locations, such as around developed areas and private in-holdings, and adjacent to the Park boundary.

Both inside and outside Park boundaries, opportunities for managing fuels will be limited in the absence of tree removal. Within the Park, logging for fuel hazard reduction may be difficult to justify, especially over a large enough area to improve future large-fire management options. Large-scale prescribed firings alone probably will not represent a cost-efficient alternative. Still, some form of fuels management will be necessary in order to lower the flammability of mature forests. Outside the Park, fuels management through timber removal is more attractive, especially when costs can be covered by higher stumpage prices. Justification may prove difficult during periods of low stumpage prices (e.g., 1988 TNF timber sales were below cost), but the wood harvest is a major driving force in the local economy.

In short, many factors beside fuels and flammability must be considered when contemplating future management options in the GYA. Clearly, the existence of Yellowstone National Park affects management options and practices in adjacent national forests. At the same time, judicious fuel management at the boundary will be essential in order to improve management options within the Park.

Acknowledgments

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Comparison of Fuel Consumption Between High Intensity and Moderate Intensity Fires in Logging Slash

Abstract

Slash burning is an integral tool of forest management in the Pacific Northwest. The purpose of this study was to determine if mass-ignited, high intensity fires had less fuel consumption than moderate intensity fires. There was 23 percent less woody fuel consumption in high intensity burns than in moderate intensity burns. A hypothetical maximum consumption rate model was derived for high intensity fires. High intensity fires could be used to reduce emissions from slash burning, thereby diminishing one of its adverse effects.

Introduction

Thousands of acres in the Pacific Northwest are burned each year as an integral part of forest management. Slash burning is used to prepare harvested sites for planting and to reduce wildfire hazards.

Air quality is directly impacted by smoke from slash fires. As a result, several studies have been undertaken to predict the consumption of fuels during slash burning. Emissions that are released into the air during slash burning can be controlled by understanding and manipulating fuel consumption.

Certain ignition techniques are shown to decrease fuel consumption (National Wildfire Coordinating Group 1985) and to improve air quality by decreasing emissions. In a 1984 pilot study, the Fire and Air Resource Management Project, Pacific Northwest Research Station, USDA Forest Service, measured fuel consumption in rapidly ignited, high intensity fires. Results from the pilot study indicated that high intensity fires consumed less fuel than did lower intensity fires, with the majority of consumption taking place during the flaming phase.

The purpose of this paper was to further investigate fuel consumption during high intensity fires. The objective was to determine if high fire intensities significantly reduce fuel consumption as compared to moderate fire intensities.

A model was developed to determine if differences in the thermal environment could explain differences in fuel consumption between high and moderate intensity fires.

Literature Review and Background

The majority of slash burns in the Northwest are ignited with hand-held torches, using strip headfires. This ignition techique involves igniting one to several adjacent strips of fuel at one time. As the fire spreads, these strips burn together in the flaming stage which is characterized by the movement of visible flame through the fuel. As the flaming front passes and the fire "dies-down," entering the smoldering stage (National Wildfire Coordinating Group 1985), the next successive strips are ignited. The process is slow, and only small areas of the unit are in the flaming stage at one time. Fire intensities (heat release per area per time) range from low to moderate, depending on the ignition rate. This paper refers to such burns as moderate intensity fires.

High intensity fires differ from moderate intensity fires in several ways, the most obvious being the method of ignition. A unit must be mass-ignited to achieve a high intensity fire (Countryman 1964). Mass ignition can be accomplished by handlighting or by helitorch; the ignited strips interact quickly, and the entire unit is simultaneously in flames. The result is longer flame lengths, which result in violent fire behavior, fire whirls, and high intensities. Brown and Davis (1973) discuss fire intensities in terms of "stair-step or a discontinuous-type" scale. They suggest this discontinuous scale occurs because fire intensity increases rather abruptly from one level to another level of considerably higher intensity. Above this abrupt step is the region of high intensity fires, often accompanied by large convection columns (Byram 1957). This paper refers to such burns as high intensity fires.

Most of the prior slash-burn consumption studies have investigated woody fuel and duff (consisting of the fermentation and humus layers) consumption from moderate intensity fires. Woody fuel consumption studies have been completed in Idaho,

Montana, and Ontario (Norum 1977, McRae 1980, Brown *et al.* 1985, Reinhardt *et al.* 1989). Duff consumption studies have been undertaken in different geographic locations and forest types (Van Wagner 1972, Shearer 1975, Norum 1977, Sandberg 1980, Brown *et al.* 1985).

The Fire and Air Resource Management Project, Pacific Northwest Research Station, has conducted several woody fuel and duff consumption studies for logging slash using moderate intensity fire in western Oregon and western Washington (Sandberg and Ottmar 1983, Ottmar 1984, and Ottmar *et al.* 1985). These studies provide a baseline against which the fuel consumption data for this study of high intensity fires will be compared. Data collected in the Fire and Air Resource Management Project studies were the most relevant to the area and conditions under which the high intensity fires were studied. To simplify the comparison between moderate intensity fires and high intensity fires, the same variables were measured and the same methodology was used.

Sandberg and Ottmar (1983) found that the best predictor of large, woody fuel[1] consumption, measured by diameter reduction, is the internal moisture of large logs. In attempting to predict fuel consumption by combustion stages (flaming and smoldering), Ottmar (1984) did a preliminary study of woody fuel that focused on predicting consumption during the flaming stage. Ward (1983) had already found that emission factors differ for flaming combustion and smoldering combustion.

Ottmar (1984) speculates that consumption of small fuels occurs mostly during the flaming stage; and that diameter reduction of large, woody fuels during the flaming stage is dependent on the amount of small fuels consumed. Ottmar suggests that the ratio of flaming versus smoldering consumption (flaming proportion) for large logs is dependent on the 100-hour[2] fuel consumption.

Consumption of duff was found to be affected by the burning of woody fuels, depending on duff moisture (Ottmar *et al.* 1985). Two different moisture conditions were found to describe two duff consumption conditions. Duff reduction for wet duff (less than 25 days since 1.3 cm of rain) is dependent on the total heat load supplied by the combustion of large woody fuels. Duff reduction for moist duff (more than 25 days since 1.3 cm of rain) is dependent on fire duration, which is determined by diameter reduction of the large fuels. Preliminary results from flaming duff consumption studies suggest that flaming duff reduction is dependent on flaming diameter reduction of woody fuel (Ottmar 1984).

Fuel consumption during high intensity fires is not well documented and is primarily qualitative rather than quantitative. The reviewed literature contains discrepancies in whether high intensity fires have more or less fuel consumption than moderate intensity fires. Several early workers observed that almost all fuel was consumed on high intensity fires (Clar and Chatten 1966, Byram 1966, Brown and Davis 1973). Other observations suggest that less fuel is consumed on high intensity fires (Hurley and Taylor 1974, Ottmar [personal communication]) or that there is no difference in fuel consumption between high intensity and moderate intensity fires (McRae [personal communication]).

What factors might exist in the thermal environment of a high intensity fire that would cause a difference in fuel consumption? One possible factor is the duration of heat supplied to woody fuel. Fire duration on several high intensity fires has been observed as being very short: from 1 to 2 hours for units ranging from 24 to 200 ha (Finnis 1970, Hurley and Taylor 1974, and Ottmar [personal communication]). Fire duration for moderate intensity fires ranges between 4 to 36 hours, with an average of 8 to 12 hours, depending on fuel moisture and time of year (Ottmar [personal communication]).

The rate of consumption could be another factor influencing fuel consumption during high intensity fires. The rate of woody fuel consumption has been measured in laboratory and field experiments, and there appears to be a wide range of consumption rates for both moderate intensity and high intensity fires per 2.5 cm of diameter reduction. Laboratory consumption rates varied from 52 minutes (Schaffer 1967) to 8 minutes (Anderson 1969, and U.S. Forest Products Laboratory 1974). Field observations of consumption rates ranged from 3.8 to 11 minutes on moderate intensity fires, to 2.5 minutes on high intensity fires (Ottmar [personal communication] and Countryman 1969).

[1]Large, woody fuels will refer to dead woody material between 7.6 and 22.9 cm in diameter.

[2]100-hour refers to a timelag fuel class for roundwood diameters of 2.5 to 7.6 cm (Deeming *et al.* 1977).

There is a disparity in previous study results concerning fuel consumption and rates of fuel consumption in high intensity and moderate intensity fires. This study seeks to resolve that disparity by determining whether there is a difference in fuel consumption between moderate intensity fires and high intensity fires.

Study Areas and Methodology

Sites were selected using the criteria of Sandberg and Ottmar (1983) and Ottmar *et al.* (1985). Sixteen clearcut units were selected for high fire intensity broadcast burns, which included three units that were burned for the 1984 pilot study on high intensity fires. Sites were located on lands belonging to the U.S. Forest Service, the U.S. Bureau of Land Management, the Oregon Department of Forestry, and cooperating private companies. One site was located in Idaho, one in Montana, six in Oregon, and eight in Washington.

Thirteen units were cable-yarded and the remaining three were tractor-logged. Second-growth Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) were the main species on 13 of the units. Two units consisted of lodgepole pine (*Pinus contorta* Dougl.) and one unit was predominantly subalpline fir (*Abies lasiocarpa* [Hook.] Nutt.).

The same variables collected in the Sandberg and Ottmar studies (Sandberg and Ottmar 1983, Ottmar 1984, and Ottmar *et al.* 1985) were collected for this study of high intensity fires. These variables were moisture content of woody fuel material; diameter reduction for both flaming and total consumption; large and small woody fuel consumption; and duff reduction, during both the flaming stage and in total.

Five of the sixteen units were eliminated from the study after the burns were carried out because of high fine fuel moistures which impeded the spread of the fire; or because of sustained winds during the smoldering stage, which increased fuel consumption (Sandberg and Ottmar 1983). The remaining eleven burns were used for statistical comparisons of fuel consumption between high intensity, moderate intensity, and non-attainment fires. Non-attainment fires are fires that did not reach high intensities. These fires are defined as non-attainment fires until it can be determined statistically if they are moderate intensity fires or outliers. The moderate intensity fires used for fuel consumption comparisons are from studies by Sandberg and Ottmar (1983), Ottmar (1984) and Ottmar *et al.* (1985).

Averages for each of the four variables in the high intensity, moderate intensity, and non-attainment fires were determined. These averages were then tested for significant differences using the 2-tailed, t-test at $\alpha = 0.05$ between non-attainment and moderate intensity fires, and between high intensity and moderate intensity fires.

The procedures from Ottmar and Sandberg (1981) and Ottmar (unpublished manuscript. Flaming consumption rates for moderate intensity fires. *On file with,* USDA For. Ser., Fire and Air Res. Mgmt. Proj., Seattle.) were used to measure flaming duration and flaming consumption rates. Flaming duration was determined by visually estimating the percentage of the area involved in the flaming stage and the time that the area was flaming. Flaming consumption rate was calculated by dividing flaming duration by flaming diameter reduction.

A hypothetical maximum flaming consumption rate for high intensity fires was derived from the conduction equation discussed in Jakob and Hawkins (1957). The measured high intensity and moderate intensity fire consumption rates were compared to the hypothetical maximum consumption rate. If the measured high intensity fire rates approach the hypothetical maximum consumption rate but do not exceed it, and there appears to be a break or step between the moderate and high intensity fire consumption rates, there would appear to be a difference in the thermal environment for high intensity fires.

Results

Of the 11 fires used for this study, 7 burned at high intensity. The remaining four fires did not burn at high intensity, and are referred to as non-attainment fires. Fuel consumption and flaming consumption rates for the high intensity and non-attainment fires are reported in Table 1.

The objective of the statistical analysis was to determine (1) if the four non-attainment fires had the same fuel consumption as the moderate intensity fires, and (2) if the seven high intensity fires had different fuel consumption from the moderate intensity fires. Woody and duff consumption from the two groups of fires, high intensity and non-attainment, were compared to the woody and duff consumption data from the moderate intensity fires.

TABLE 1. Summary of woody fuel and duff consumption.

Name	Diameter Reduction (cm)	Flaming Proportion (%)	Duff Reduction (cm)	Flaming Duff Reduction (%)	Flaming Consumption Rate (minutes/2.5 cm)
High Intensity Fires					
Little Deschutes	1.8	1.0	3.0	1.2	*
Twin Harbors	4.0	1.0	4.0	1.9	*
High Divide	2.3	1.0	1.6	0.6	*
Winston #5	2.7	1.0	1.8	*	*
Summit Lodgepole	7.4	0.9	3.6	2.4	3.1
Low Donovan	4.7	0.9	2.5	1.0	2.8
Sprucedale	4.8	1.0	4.9	2.0	2.8
AVERAGE	4.0	1.0	3.1	1.5	2.9
Non-attainment Fires					
Davis Creek	4.7	0.6	2.9	0.9	5.0
Sweethome Area #2	4.8	0.6	3.9	1.5	*
Sweethome Area #3	8.1	0.9	4.5	1.9	*
Creel Rock	6.2	0.5	4.4	1.4	4.3
AVERAGE	6.0	0.7	3.9	1.4	4.7

*Data not collected

The four fuel consumption variables used for comparison between the groups were diameter reduction, flaming proportion (proportion of flaming diameter reduction to total diameter reduction), duff reduction, and flaming duff reduction. Diameter reduction is dependent on fuel moisture, flaming proportion is dependent on 100-hour timelag fuel consumption, duff reduction depends on large woody fuel consumption, and flaming duff reduction is dependent on flaming diameter reduction. Because of these dependencies, only those moderate intensity fires which fell within the range of the independent variables for either high intensity fires or non-attainment fires were used.

All four consumption variables for non-attainment fires were determined to have no significant differences from moderate intensity fires (Table 2), and are assumed to belong to that group. High intensity fires had significantly higher flaming proportion and significantly less diameter reduction than moderate intensity fires (Table 2). Hence, woody fuel consumption was 23 percent less for high intensity fires than for moderate intensity fires. Flaming and total duff consumption for high intensity fires are statistically the same as those for moderate intensity fires for the range of large woody fuel consumption investigated.

Discussion

Flaming proportion was higher for high intensity fires than for moderate intensity fires. This suggests there is very little smoldering during high intensity fires because flaming proportion is dependent on 100-hour consumption, which primarily takes place during the flaming stage. Yet, the statistical analysis suggests that total fuel consumption is less (Table 1). What is limiting fuel consumption during high intensity fires? Brown and Davis (1973) suggest that heat conduction controls consumption of fuel in logging slash. Based on this assumption, a model of heat conduction into large fuels during high intensity fires was developed for this study.

The variables that control conduction on an infinitely thick wooden slab during a sudden change in temperature are time, temperature, and diffusivity (Jakob and Hawkins 1957). It is assumed that diffusivity will not change between moderate intensity fires and high intensity fires. Average surface temperatures of logs fluctuate in high intensity fires, which affects the conduction equation, but the equation is not overly sensitive to changes in temperature. Therefore, it is hypothesized that time—how long heat is supplied to the surface of the large fuel—must be the main limiting variable.

TABLE 2. Summary of statistical t-test results.

	Sample Size	Mean (cm)	Significant Difference (alpha = 0.05)
Diameter reduction			
Non-attainment fires	4	5.9	no
Moderate intensity fires	14	6.3	
High intensity fires	7	3.6	yes
Moderate intensity fires	10	6.1	
Flaming Proportion			
Non-attainment fires	4	0.65	no
Moderate intensity fires	11	0.68	
High intensity fires	7	0.98	yes
Moderate intensity fires	17	0.53	
Duff Reduction			
Non-attainment fires	4	3.9	no
Moderate intensity fires	6	3.4	
High intensity fires	7	3.1	no
Moderate intensity fires	19	2.3	
Flaming Duff Reduction			
Non-attainment fires	4	1.4	no
Moderate intensity fires	9	1.5	
High intensity fires	6	1.5	no
Moderate intensity fires	13	1.4	

During a high intensity fire, a given amount of flaming consumption occurs during a shorter period of time than during a moderate intensity fire: the flaming consumption rate is faster. High intensity fires are mass-ignited, so small fuels burn rapidly, producing high intensities. Therefore, the surface of the large fuels is intensely heated for only a short time, creating a steep temperature gradient within the log. This steep temperature gradient causes moisture to be driven off and the log surface to be consumed almost simultaneously. Once the small fuels are consumed, the flaming stage is over and consumption of the large fuels stops because consumption to the depth to which moisture was driven off has already occurred. Because the flaming consumption rate is faster and consumption is limited to the flaming phase, there is less total woody fuel consumption.

Conversely, during a moderate intensity fire, a given amount of flaming consumption occurs during a longer period of time. Therefore, the flaming consumption rate is slower than during a high intensity fire. Heat is supplied to the surface of the large fuels over a longer period of time and a deeper temperature gradient is developed, drying the log to a greater depth. When the small fuels stop burning in the flaming stage, the larger fuels continue to smolder to the depth to which they have been dried. This is due to a slower flaming consumption rate, so consumption occurs not only during the flaming phase but during the smoldering phase as well. Consequently, there is more total fuel consumption.

A hypothetical maximum consumption rate model was developed for high intensity fires, using the Jakob and Hawkins (1957) conduction equation, to quantitatively determine if time is limiting consumption.

The equation is deemed appropriate for use with high intensity fires even though slash burning may violate some of the assumptions. For example, heat is not being conducted into an infinite slab. Also, the temperature at the log surface is not constant but is widely fluctuating. The equation is considered sufficiently robust to overcome these inconsistencies.

To develop the model of maximum consumption rate, a minimum depth or thickness must be determined to which a log must be preheated before the initiation of flaming combustion. Frandsen (1973) describes an effective heating number which yields the proportion of the particle (thickness of the shell) that has to be heated before ignition as a function of particle size. Frandsen's equation predicts that, as particle size increases, the effective heating number decreases. The proportion or thickness of the shell necessary to heat the particle can be graphed against the diameter of the particle using Frandsen's equation. As the size of the particle increases, the thickness of the shell rises sharply, peaks, then gradually decreases. However, Frandsen only collected data for particles less than 1.3 cm in diameter, the diameter at which the curve of the graph peaks. For the thickness to actually decrease does not make intuitive sense and was determined only mathematically, not empirically. I propose—in a physical sense of the problem—that the thickness sharply increases, reaches a peak, and levels off. At this leveling-off point, the thickness ranges from 0.08 to 0.18 cm, depending on whether the particle is heated from all sides or from one direction. Assuming that this value holds true for all particles larger than 1.3 cm, the average of 0.08 cm and 0.18 cm was used as the minimum thickness to be heated before ignition.

The conduction equation is as follows (Jakob and Hawkins 1957):

$$\frac{t_x - t_s}{t_i - t_s} = \text{erf}\left(\frac{x}{2\sqrt{\alpha T}}\right),$$

where the variables are as follows:

t_i is initial surface temperature before heating,
t_s is temperature to which the surface is raised,
t_x is temperature at the depth x in the log,
α is diffusivity of wood,
x is the radial distance into the log from the surface,
$\text{erf}\left(\frac{x}{2\sqrt{\alpha T}}\right)$, is Gauss' error integral, and
T is the time it takes to reach x at a specified t_x.

To develop the maximum consumption rate, the following values are assumed:

$t_i = 21°C$,
$t_s = 925°C$, an estimated average temperature for the surface of the log during the flaming stage for high intensity fires,
$t_x = 343°C$, minimum temperature at which flames appear when rapid heating takes place (Brown 1951),
$\alpha = 1.6*10^{-4}\text{cm}^2$ per second (U.S. Forest Products Laboratory 1974).
$x = \frac{0.08+0.18}{2} = 0.13$ cm, minimum thickness needed before flaming combustion.

Since $\text{erf}\left(\frac{x}{2\sqrt{\alpha T}}\right) = \frac{t_x - t_s}{t_i - t_s} = 0.6438$,

then $\frac{x}{2\sqrt{\alpha T}} = 0.65$.

Solving for T:

$$T \cong \frac{x^2}{1.69\alpha}$$

Substituting the values for x and α:

$T \cong 6.0$ seconds.

The hypothetical maximum consumption rate for high intensity fires is 0.13 cm of diameter reduction in 6.0 seconds, or 2.5 cm of diameter reduction in 2 minutes.

Plotting this maximum consumption rate on a graph with moderate intensity flaming consumption rates shows that the high intensity flaming consumption rates are approaching, but not exceeding, the maximum high intensity flaming consumption rate (Figure 1). As a group, moderate intensity rates are slower than the measured high intensity group and hypothetical maximum high intensity rates. There is, therefore, a different consumption rate—faster—for the group of high intensity fires than for the moderate intensity group. This supports the qualitative interpretation made previously. However, this model cannot be tested against the observed high intensity fire rates due to insufficient data.

No evidence was found for the discontinuous jump in intensity suggested earlier between moderate intensity fires and high intensity fires. Examining the graph shows no stair-step or break between the moderate intensity fires group and the high intensity fires group, but rather there seems to be a continuous range of variation. This indicates that, as the flaming rate of consumption increases, the total fuel consumption decreases, depending on a subjective classification of increasing intensities.

The results from this study were based on only seven high intensity fires. This small sample size suggests that it is difficult to achieve high intensity fires under the moderate moisture conditions used in this study. The reason for this may be that many variables affecting a burn cannot be controlled. One example is the difficulty in having a large area in the flaming stage simultaneously. Another example is that many weather variables, such as wind, rain, fuel moisture, and atmospheric stability, can affect the way a slash fire will burn.

Conclusion and Recommendations

Mass-ignited, high intensity fires are difficult to achieve. For this reason, the results of this study were based on a small sample size. Mass-ignited, high intensity fires are shorter in duration and have a faster flaming consumption rate than moderate intensity fires. This faster flaming consumption rate suggests that the thermal environment for high intensity fires differs from that for moderate intensity fires. Because of this difference, high intensity fires have less fuel consumption than moderate intensity fires.

These units were operational burns where a fire manager had determined the burn plan. As in all operational burns, it is difficult to control all the variables that determine whether a high intensity fire will be achieved. Evidence of this fact was that only 7 out of 16 burns reached high fire intensities.

Still, I believe that the method of burning with high intensity fire is a viable tool which the land manager can use to reduce fuel consumption. It could be possible for the manager to evaluate several variables that would determine what level of intensity is needed to achieve a high intensity fire.

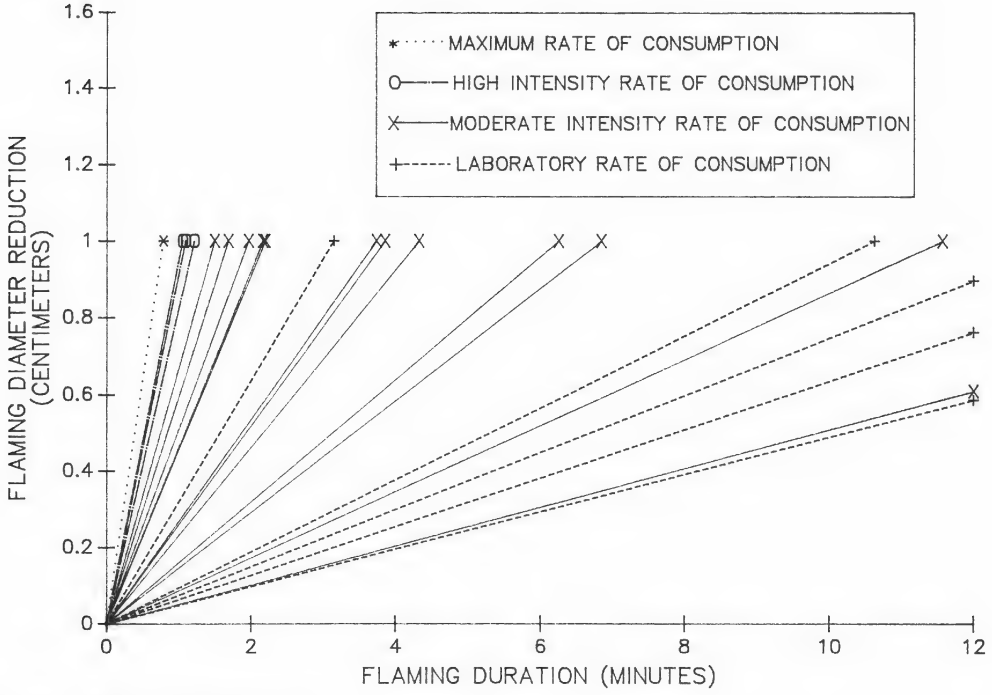

Figure 1. Flaming consumption rates.

From these variables, a classification of intensities could be determined which would be a factor in the calculation of fuel consumption. Size of unit, ignition method, length of time to ignite unit, fine fuel moisture, and the formation of a large convection column are the variables needed. Because there is less fuel consumption during high intensity fires this would lead to a reduction in the reported total fuel consumption. Since this method reduces fuel consumption, this burning technique could be used by air quality personnel to give credit for less emissions.

Several of the assumptions made in this study could be further investigated. One such assumption was the minimum thickness derived from Frandsen's effective heating number. A better approximation of minimum thickness needs to be investigated because the number was extrapolated from particles that were smaller than those used in this study. I would suggest conducting a laboratory study for determining the minimum thickness needed to be heated before ignition for larger particle sizes.

Since the measure of intensities was very subjective, another approach for determining fire intensities should be studied. A more quantitative approach for determining the thermal environment surrounding large, woody fuels should be developed. One possible approach would be to measure the radiation to which the log is subjected and from this measurement the intensity of the fire could be determined.

Knowledge of a fire's intensity would provide managers with yet another tool to estimate fuel consumption for prescribed burning.

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Burning Rate of Smoldering Peat[1]

Abstract

Smoldering ground fires spread slowly (about 3 cm h^{-1}) and can raise mineral soil temperatures above 300°C for several hours with peak temperatures near 600°C, resulting in decomposition of organic material and the death of soil organisms. Smoldering ground fire has potential for reigniting surface fire long after the main front has passed. The rate of smoldering was examined with Canadian sphagnum peat moss as a representative fuel. The time to burn a known amount of organic mass was monitored for different organic bulk densities and moisture and inorganic contents. Organic bulk densities were comparable to the field and ranged from 90 to 180kg m^{-3}. Moisture and inorganic contents were expressed as mass ratios relative to the organic mass and covered the range of sustained smoldering combustion. Moisture ratios, R_M, ran up to 0.8 and inorganic ratios, R_I, up to 4.0. The burning rate is independent of the organic bulk density. A universal burning rate, the unit area burn rate (UBR), was obtained by normalizing the burning rate to the area of the burning surface. It is expressed as follows:

$UBR = 0.27 - 0.097\ R_M - 0.033(R_I - D)$ g cm^{-2} h^{-1}, where $D = R_I$ if $R_I < 1.0$, and $D = 1.0$ if $R_I \geq 1.0$.

Introduction

Smoldering, although not as visually dramatic as flaming combustion, is an important component of forest fires. It is common in the duff of the coniferous forest that is derived from the accumulation of detritus. The duff includes the fermentation and humus layers or the O_e and O_a soil horizons that lie between the surface litter and the mineral soil (Brady 1984). The rate of smoldering—mass loss over time—and its dependence on organic bulk density, moisture, and inorganic content of the duff is the topic of this manuscript.

Smoldering is a form of fire spread that generally occurs in fuel arrays that are more tightly packed than those that sustain flaming. A transition from flaming to smoldering is expected when fuel particles are thin or very small in diameter and occupy more than approximately 10 percent of the volume. Rothermel (1972) shows a decreasing reaction intensity, the rate of heat release of spreading fire per unit area of the forest floor, that extrapolates to very low values when the packing ratio or fractional volume occupied by fuel approaches 10 percent. Forest duff, which has packing ratios greater than 10 percent, exhibits only smoldering, while litter, with packing ratios less than 10 percent, exhibits only flaming. (A form of smoldering does occur in large fuels independent of packing during the glowing phase in large fuel pile burning, but is not addressed here.)

The ground fire, as the smoldering fire is named by fire control specialists, presents no threat in terms of its rate of spread. However, it can persist for days or weeks and later can initiate a flaming surface fire if it is fanned into flames by a chance gust of wind (Wein 1981). This potential has branded the ground fire as the "hold-over fire." Smoldering duff temperatures in excess of 300°C have been observed for up to 12 hours under a mixed overstory of western larch (*Larch occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) (Hartford and Frandsen, in press).

The duff presents an effective barrier to the transfer of heat to the mineral soil during passage of a surface fire. However, if the duff is ignited, the resultant smoldering fire is likely to be brought into direct contact with the mineral soil raising its temperature above 300°C for several hours. Flora and fauna of the duff are consumed along with roots and seeds. Organic material in the upper portion of the mineral soil is oxidized, and roots, seeds, and soil organisms necessary for recycling nutrients are killed and possibly consumed. Smoldering duff can also contribute more than 50 percent of the air pollutants produced from a fire (Sandberg 1983). If, on the other hand, the moisture and inorganic content of the duff exceeds the limits for combustion then the duff is likely to remain unburned and not act as a source of heat (Frandsen 1987). Under these conditions the smoldering combustion zone is prevented from coming into

[1]Based on Ph.D. dissertation submitted to the University of Montana.

direct contact with the mineral soil. However, the moisture limit may be overcome. A flow of heat from an abundance of surface fuels (slash) burning at the surface can dry the fuel and bring it within the combustion limits.

Smoldering can be initiated in the duff after a fire spreads through the forest litter if the duff is capable of sustained smoldering (Frandsen 1987). Larger litter fuels that sustain burning, such as twigs and cones, are ignited and act as centers to propagate the fire down into the duff. Once the fire is established, it propagates horizontally and vertically until it reaches conditions that will not sustain smoldering.

If heat from the smoldering combustion wave is not sufficient to overcome the heat of vaporization required by moist fuel, smoldering must cease. Furthermore, inorganic materials within the fuel matrix can absorb heat but not oxidize to produce more heat. Thus, the amount of heat produced per unit volume is reduced. Both moisture and inorganic content should reduce the effectiveness of the available heat to propagate the smoldering fire. Smoldering is expected to proceed with the greatest rate when these inhibiting variables have their minimum values.

The factors that may affect the rate of burning are the moisture and inorganic content of the duff and its organic bulk density. Both the moisture and the inorganic content hinder the smoldering process and therefore are viewed as slowing down the rate of burning. Increasing the bulk density may slow down the supply of oxygen to the combustion interface and also slow the rate of burning. However, Ohlemiller *et al.* (1979) found with flexible polyurethanes that "the smolder process is flexible enough to adapt to a wide range of oxygen supply levels, including extraordinarily low levels." The following procedure outlines an experiment to measure the dependence of the mass consumption rate of smoldering peat on the above factors.

Methods

Canadian sphagnum peat moss was selected as a representative fuel for examining the rate of smoldering in the laboratory under simulated field conditions. It has similar particle sizes and bulk and particle densities as duff, is an important ground cover in the wet boreal forest that supports smoldering combustion (Wein 1983), and is a uniform fuel that is commercially available. The range of organic bulk densities varied from 90 to 180 kg m^{-3}. This corresponds to the range that is normally found in duff (Woodard and Martin 1980; Harrington 1986). Results are related to smoldering in the absence of wind and slope.

The moisture and inorganic contents were expressed as mass ratios relative to the organic mass. The moisture ratio, R_M, ranged from 0 to 0.8 at 0.2 intervals and inorganic ratio, R_I, from near 0 (natural peat inorganic ratio) to 4 at intervals of 1. All combinations were sampled except those that were outside the smoldering limit given by Frandsen (1987) (Figure 1), as

$$R_M + (R_I/4) < 1.1 \quad (1)$$

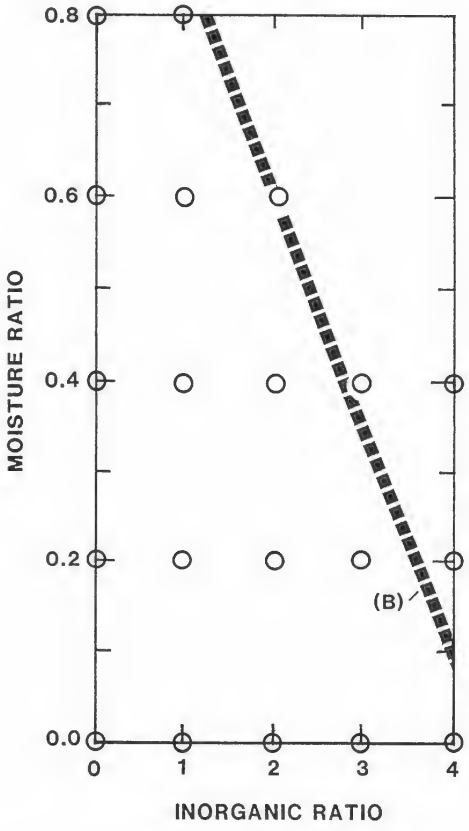

Figure 1. Sampling design. Each circle designates a sampling combination of moisture and inorganic ratios for each organic concentration. Each combination was replicated three times. Few observations were attempted beyond the expected smoldering limit (B).

Peat was moistened or dried to reach the selected moisture ratios. Inorganic material in the form of 240 mesh (56 μ particle size) powdered silica was added to moist peat to obtain inorganic ratios higher than the inherent inorganic content of peat. Silica was used to ensure that there would be the least amount of chemical interaction between the added inorganic material and the combustion process. It is speculated that natural inorganic material occurring in peat may react in a manner to alter the combustion process. More detail on sample preparation can be found in Frandsen (1989).

The experimental sample was contained within a noncombustible insulated box with an open top. The box was placed in a sealed glass cylinder. The cylinder was sealed except for an inlet and exit to allow for a flow of air. The flow was held constant at 3.5 g min^{-1} (near 3.5 ℓ min^{-1}), an amount that was determined to be sufficient to maintain smoldering without oxygen starvation, as experienced in the field. The sample volume within the insulated combustion box was 5 cm x 5 cm in cross-section and 4 cm deep. The walls were 2.5 cm thick. The insulating material was ceramic board with thermal properties similar to peat (Frandsen 1987). Consequently, the heat transferred to the walls was not greatly different from the heat transferred within the peat. This allowed the burning peat to approximate part of an expanded volume. There was no excessive heat loss or cooling at the walls of the container, as evidenced by the absence of unburned peat adjacent to the walls.

The upper exposed surface of the peat was ignited by four rows of resistance coils heated to a red glow. The glowing area approximated the area of the peat surface and was held within 5 mm of the surface for 2 minutes. Prior experimentation indicated that 2 minutes was sufficient to ignite peat at all combinations up to the highest moisture and inorganic ratios. The amount of organic material consumed under enhanced burning during the ignition period is small compared to the total mass consumed. Consequently, there is little error in the total burn time of the sample that ranged from 80 to 257 minutes.

The igniter coils were lifted away from the peat surface within 15 seconds of switching off the igniter. The duration of smoldering was taken from the time the igniter was switched off until smoldering stopped as evidenced by the absence of carbon monoxide in the air flowing from the cylinder containing the smoldering peat. Carbon monoxide was considered absent when the volumetric concentration was less than 0.0005 V/V.

Results

Data were obtained from 172 sample observations. This includes additions to the original design for comparison samplings and losses due to those conditions that would not sustain combustion.

The average smoldering burn rate was calculated by dividing the organic mass (sample mass – inorganic mass) by the duration of smoldering. The organic mass was equivalent to the total mass lost because all of the organic mass was consumed during smoldering.

There is a general trend toward lower burn rates with increasing inorganic ratios above 1.0 for each moisture ratio (Figure 2). Burn rate variations within replications of the organic bulk density were as great or greater than variations between organic bulk densities. Hence, there is no dependence on the organic bulk density. Because of this independence, one may view each combination of the moisture and inorganic ratios as replicated by as much as 12 times if all burns were successful.

Two commercial varieties of peat were used. The original choice was used for all pilot experiments and initial observations at moisture ratios of 0 and 0.2. When additional peat was needed, no more of that variety was available. A replacement was used at moisture ratios of 0.4 through 0.8. The search for the replacement included those peats having similar bulk physical properties and the lowest inorganic content approaching that of the original peat. Comparisons of the burn rates showed the two peats to be equivalent at 0 moisture ratio, but the burn rate of the original peat was 20 percent greater at the larger moisture ratios (0.4 to 0.8). Observations with the replacement peat were adjusted upward by 20 percent so that they could be used to complement the original observations (Frandsen 1989).

Noting that the burn rates at inorganic ratios near 0 and at 1 show little difference at moisture ratios 0 through 0.4 (Figure 2), we can linearize the burn rate by combining the burn rates at 1 with those near zero and giving the combined inorganic ratio a dummy value of 0 and reducing all the higher inorganic ratios by 1. (This is not the case for moisture ratios 0.6 and 0.8 but the data at moisture ratio 0.6 account for only 14 percent of the data and only 2 percent at 0.8 moisture ratio.)

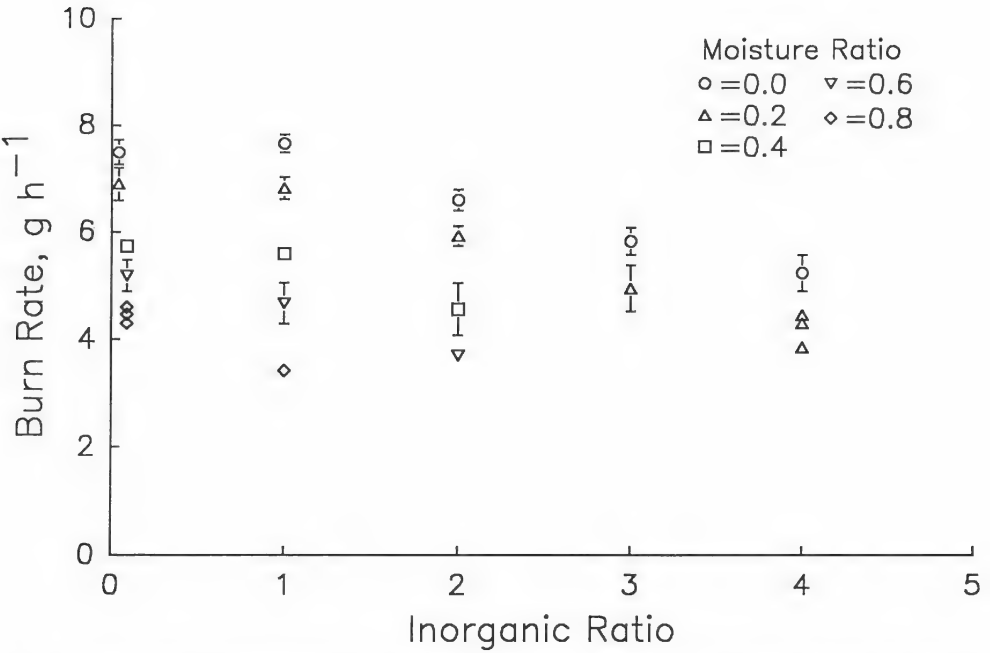

Figure 2. Burn rate dependence on the inorganic ratio at moisture ratios of 0 to 0.8. Note the decline of the burn rate with increasing inorganic ratio beginning at 1. Error bars relate to the standard deviation, n = 6 to 12 observations. Since observations have no error bars except for moisture ratio 0.4 at inorganic ratios of 0.09 and 1 where the error is less than the symbol size. (1 g h^{-1} = 2.78 x 10^{-7} kg s^{-1})

The modified data have the appearance of being linear in both the inorganic and moisture ratios. A linear model developed by applying a least squares fit to the modified data is shown below. It also embraces the shift in the inorganic axis discussed above.

$$BR = 7.58\text{-}2.72R_M - 0.918(R_I - D) \quad g\ h^{-1}$$
$$(1\ g\ h^{-1} = 2.78 \times 10^{-7}\ kg\ s^{-1}) \qquad (2)$$

where BR = burn rate

and $D = R_I$ if $R_I < 1.0$

$D = 1.0$ if $R_I \geq 1.0$

The burn rate versus moisture ratio is shown in Figure 3, along with the linearized model. The percentage error (predicted−actual)/actual, is shown over the range of inorganic ratios at a moisture ratio of 0 in Figure 4. Estimates of the burn rate from the linear model indicate that 91, 89, and 90 percent of the predicted values lie within ± 10 percent of the actual value for moisture ratios of 0, 0.2, and 0.4. Errors are greater at moisture ratios of 0.6 and 0.8. Only about 70 percent of the predicted values were within ± 10 percent of the actual values. The lower predictive capability is not surprising considering the departure of these data from the form of the data at the lower moisture ratios in Figure 2. Furthermore, these data, as mentioned above, account for only 14 and 2 percent of all the observations.

Discussion

Many people think in terms of the linear spread rate of smoldering when reference is made to burn rate, rather than to the mass loss burn rate presented here. We gain insight into the spread rate if we convert the burn rate to a unit area burn rate by normalizing the burn rate to the area of the burning surface of the smoldering wave. The resulting unit area burn rate relates to the smoldering wave and is independent of the combustion box.

The cross-sectional area, A, of the burning volume of the combustion box (Figure 5) approximates the burning surface as it moves downward. The linear spread rate can be obtained by equating the mass loss burn rate, $\Delta m/\Delta t$, to the product of the organic bulk density, ρ_o, and the volume

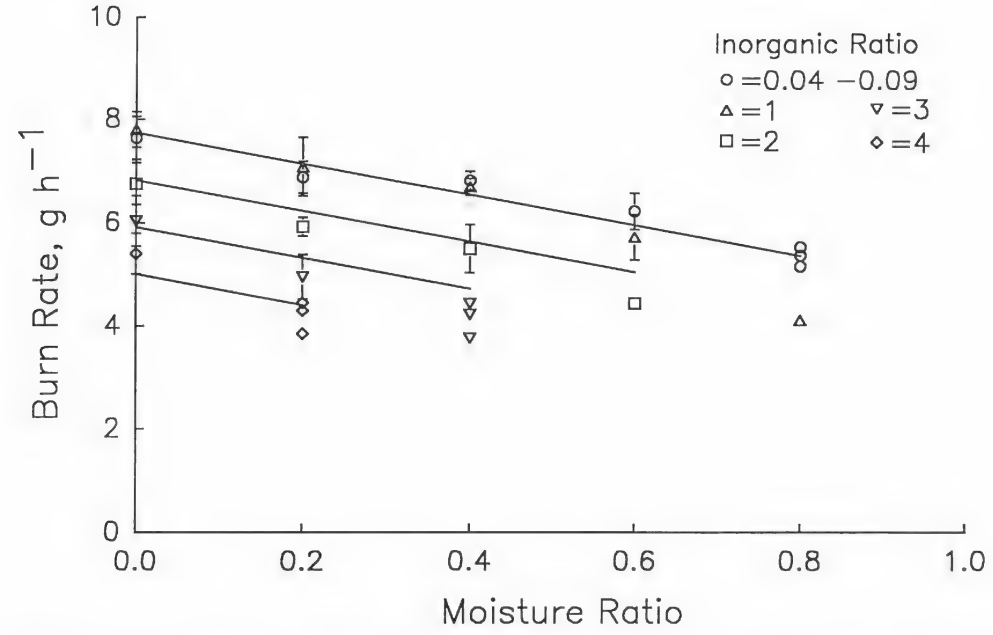

Figure 3. Linear least squares fit to observations. Error bars relate to the standard deviation, n = 6 to 12 observations. Single observations have no error bars. Note single linear fit to inorganic ratios from 0.04 to 1. (1 g h^{-1} = 2.78 x 10^{-7} kg s^{-1})

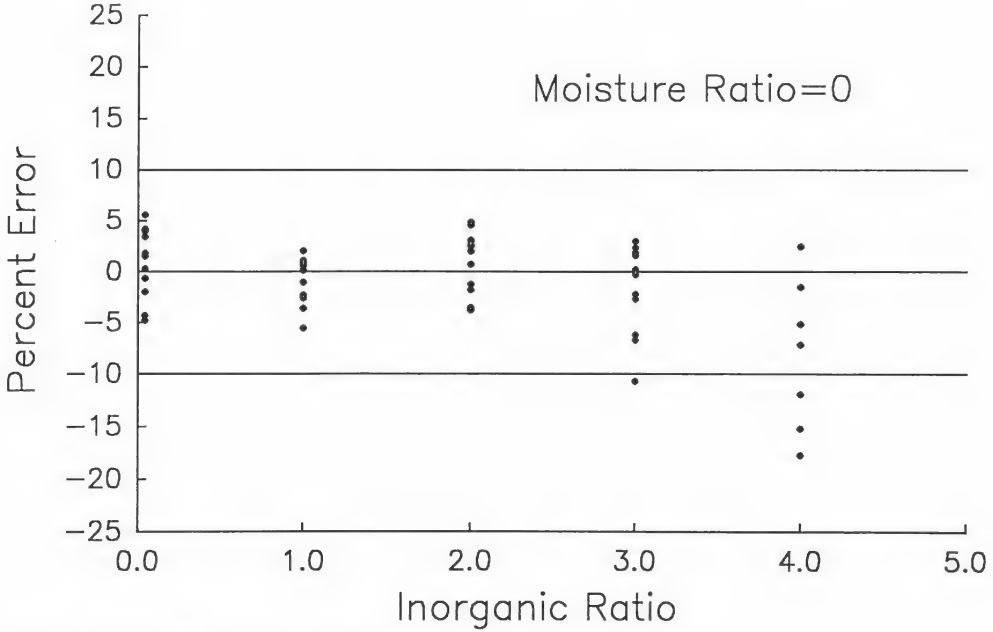

Figure 4. Errors in predicting the burn rate. N = 58.

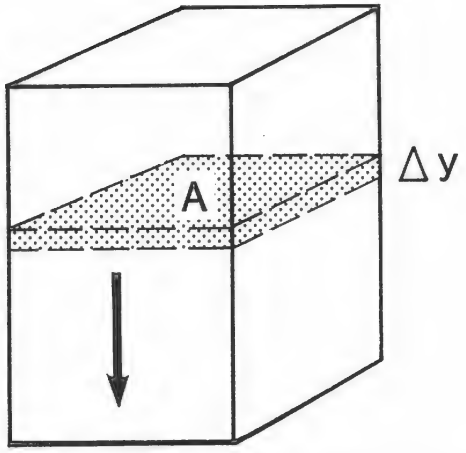

Figure 5. The burning volume within the combustion box showing the burning surface, A, as it moves downward a distance, Δy, sweeping out a volume element, ΔV = AΔy.

consumption rate, $A\Delta y/\Delta t$, as swept out by the burning surface in Figure 5.

$$\Delta m/\Delta t = \varrho_o A \Delta y/\Delta t \quad g\ h^{-1} \qquad (3)$$

Transposing, we have the linear rate of spread

$$\Delta y/\Delta t = ((\Delta m/\Delta t)/A)/\varrho_o \quad cm\ h^{-1} \qquad (4)$$

where $\Delta m/\Delta t$ is the burn rate, BR
and $(\Delta m/\Delta t)/A$ is the unit area burn rate , UBR

Although the box was designed for a cross-sectional area of 25 cm^2, the actual area increased slightly from deterioration of the walls with each burn. Three boxes were used during the experiment to ensure that the area did not depart greatly from the designed area of 25 cm^2. The area ranged from 26 to 30 cm^2. The median, 28 cm^2, was used to approximate the area of the burning surface. Refinements in estimating the area are precluded by uncertainties in the shape of the surface. The unit area burn rate is a universal parameter that relates only to the burning surface of the smoldering wave and is expressed as the mass loss rate per unit area of the burning surface.

UBR = BR/28
Replacing BR with equation (2)

$$UBR = 0.27 - 0.097\ R_M - 0.033 R_I - D) \quad g\ cm^{-2}\ h^{-1} \qquad (5)$$
$$(1\ g\ cm^{-2}h^{-1} = 2.78 \times 10^{-3}\ kg\ m^{-2}s^{-1})$$

where UBR = unit area burn rate

and $D = R_I$ if $R_I < 1.0$
$D = 1.0$ if $R_I \geq 1.0$

UBR ranges from about 0.15 to 0.30 g cm^{-2} h^{-1}. Using a common value for the organic bulk density, 0.1 g cm^{-3} in Eq. (4), we arrive at a range of 1.5 to 3.0 cm h^{-1} that is in the right order of magnitude for smoldering (Wein 1983).

Note that in Eq. (4) the burn rate is related directly to the linear spread rate through the organic bulk density (A is constant). If the density is halved, the linear spread rate must be doubled to maintain the same mass loss rate. This is reasonable when you consider that a combustion front must pass through a less dense fuel array faster than through a more dense array to consume mass at the same rate. It should be clear that the linear spread rate may be thought of as volumetric burn rate as the burning surface sweeps out volume, but it cannot be thought of in the same sense as the mass burn rate.

Probable error analysis was employed to examine the variability of the independent variables (Frandsen 1989). Traditional statistical methods are not applicable when the sample is prepared to achieve preselected values of the independent variables as designed in Figure 1. Based on this analysis, the moisture ratio has an error that is no greater than 3.2 percent, the error in the organic bulk density is no greater than 3.5 percent, and the inorganic ratio has an error no greater than 2.6 percent.

Approximately 90 percent of the predictions from the linear model are within ±10 percent of the actual value at moisture ratios of 0, 0.2, and 0.4. Nearly all errors greater than ±10 percent are at the higher inorganic ratios. The predictive capability drops to around 70 percent at moisture ratios of 0.6 and 0.8. The preponderance of data are at the lower inorganic ratios, at and below 1. This is a reflection of limited sustained smoldering and uncertainties when approaching the combustion limit (Frandsen 1987) at moisture ratios at and above 0.4. It is likely that whatever orderliness there may be in the relationship breaks down as that boundary is approached.

The results of this study define the dependence of the rate of burning on the moisture and inorganic content of smoldering duff-like material and show a lack of dependence on the organic bulk density. A simple model capsulizes these characteristics so that inferences can be made about the rate of smoldering. These results contribute to a better understanding of the combustion of smoldering duff.

Acknowledgements

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Fuel Consumption and Fire Behavior Associated with Prescribed Fires in Sagebrush Ecosystems

Abstract

Total aboveground biomass (fuels), fuel moisture content, weather conditions at the time of burning, fire behavior, and quantities of biomass consumed by fire were measured in basin big sagebrush (*Artemisia tridentata* subsp. *tridentata* Nutt.) dominated ecosystems at the John Day Fossil Beds National Monument, Oregon. Two fire treatments were investigated: an early fall burn (September 1987, n = 4 plots), and a late spring burn (May 1988, n = 5 plots). Fires in the fall treatment plots had greater flame length (4.1 m compared to 1.7 m in spring units), rate of spread (1.6 compared to 0.3 m/s), fireline intensity (6,400 compared to 880 kW/m), and total heat load (18,120 compared to 9,270 kJ/m^2). Reaction intensity and heat-per-unit-area were not significantly different. Mass of fuel consumed was significantly greater in the fall burn units (9.8 compared to 5.2 Mg/ha). However, percent consumption was not significantly different: 93 percent in fall units compared to 84 percent in spring units. There are fundamental differences in fire behavior and fuel consumption between spring and fall burning. Differences in parameters associated with active flaming are interpreted to be largely a result of differences in fuel moisture, while differences in fuel consumption and total energy are thought to be related to fuel availability.

Introduction

In order to ascertain the effect of a fire on the biotic elements of an ecosystem, quantification of the inherent variability of the fire is of paramount importance. Fires may vary in biomass consumption and flame characteristics (i.e., fire intensity) which would in turn cause variable influences on nutrient losses, plant mortality, and postfire succession. A description of fire behavior in quantitative terms allows for correlations with observed postfire effects, as well as comparisons between studies (Alexander 1982, Rothermel and Deeming 1980). A major shortcoming in many studies of fire effects on ecosystems has been the lack of quantification of the fire itself; experimental fires are either only noted for their occurrence, or described qualitatively with nonstandard descriptors such as "cool" or "hot" (Rothermel and Deeming 1980).

Fire in basin big sagebrush (*Artemisia tridentata* subsp. *tridentata*) communities are typified as stand replacing; virtually all aboveground biomass can be consumed by fire (Kauffman and Sapsis 1989). Although many researchers have developed methods for estimating big sagebrush biomass (Brown 1976 and 1982, Frandsen 1983, Martin *et al.* 1981, Rittenhouse and Sneva 1977), none have estimated total aboveground biomass of the sagebrush ecosystem. In addition to the biomass of the big sagebrush, the fuel loading in this ecosystem would include herbaceous materials, organic horizons, dead standing and downed wood debris and other shrubs or suffrutescents. Similarly, few studies in big sagebrush-dominated ecosystems have actually quantified fire behavior parameters. Much of the previous work on fire effects in sagebrush ecosystems has been based on after-the-fact observations of the burned vegetation (Blaisdell 1953, Conrad and Poulton 1966, Uresk *et al.* 1976, 1980) or on artificial application of fire to individual plants (Britton *et al.* 1981, Wright 1971, Wright and Klemmedson 1965). Zschaechner (1985) measured fire and fuel loads, but did not record fuel consumption. Extensive documentation of fuel, weather and fire characteristics have been accomplished in research of other rangeland systems (Clark *et al.* 1985, Roberts *et al.* 1988).

As a consequence of inadequately describing fuel and fire characteristics in quantitative terms, knowledge of the ecological role of fire is limited because of the difficulty in comparing results of different studies (Martin 1984). Alexander (1982) stated that quantitative descriptions of fire behavior are not so useful in their exact description of the energy release process of the fire, but rather in providing information that will enable future researchers/managers the ability to accurately predict the effects of a given fire treatment. Therefore the objective of this study was to quantify total aboveground biomass and to investigate the variable nature of fuel consumption and fire behavior in

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basin big sagebrush-dominated ecosystems resulting from burning under different levels of fuel moisture and plant phenology.

Methods

All research burns were conducted in basin big sagebrush/perennial bunchgrass communities at John Day Fossil Beds National Monument, in eastern Oregon (USGS 15' series "Picture Gorge"; T 11 S, R 26 E, sections 31 and 32). The sagebrush understory was dominated by Idaho fescue (*Festuca idahoensis* Elmer) and bluebunch wheatgrass (*Agropyron spicatum* (Pursh.) Scribn. & Smith). All units were established on north slopes, ranging from 20 to 60 percent. Elevations ranged from 700 to 860 meters. Soils were classified in the Simas-Tub association of very stony clay-loam soils, that occur on moderately deep and well drained slopes (USDA Soil Conservation Service 1981). Mean annual precipitation (1978-1988) at a permanent weather station (approximately 2 km away from the study site) was 29 cm.

This study was established in a completely randomized design, with four replicates of a fall burn treatment, and five replicates of spring burn treatment. Size of each unit was at least 30 x 50 m, with the long axis oriented along the direction of slope.

Prefire herbaceous and downed woody fuels were measured in each unit by clipping and collecting all material in ten 30 x 60 cm plots located every two meters along a randomly located 20 meter transect. The fuels collected in these plots were partitioned into the following categories: grass/herb-live, grass/herb-dead, woody debris 0-0.62 cm in diameter (1-hr timelag), woody debris 0.63-2.54 cm in diameter (10-hr timelag), and woody debris 2.55-7.62 cm in diameter (100-hr timelag). These woody fuel size classes correspond to the standardized fuel particle size classes of the National Fire Danger Rating System (Deeming *et al.* 1977).

Sagebrush cover was estimated by line-intercept along five 15 m transects in each unit (Canfield 1941), and live and dead sagebrush density was measured in 1 x 15 m macroplots placed adjacent to the line transect. The height and elliptical crown area of all live sagebrush plants intercepting the line transects were measured. Elliptical crown area for each shrub was calculated as:

$$A = (W_1 * W_2 * \pi)/4$$

where A = crown area, W_1 = longest crown dimension, and W_2 = the longest crown dimension perpendicular to W_1. Shrub volume was calculated by multiplying crown area by maximum shrub height. These values were then averaged for each transect, and used to calculate sagebrush biomass utilizing multiple regression equations (J. B. Kauffman, D. Cummings, and K. Till, unpublished data, Dept. Rangeland Resources, Oregon St. Univ.). Utilizing shrub volume, height and/or crown area as independent variables, these equations partition sagebrush biomass into the following categories: foliage, 1-hr live, 10-hr live, 100-hr live, and attached dead (no size differentiation). Total biomass of sagebrush was then calculated by multiplying the mean loads per plant by the density of shrubs measured in the 1 x 15 m belt macroplots.

To quantify biomass of standing dead woody debris, 50 standing dead sagebrush plants were randomly harvested and weighed from an area adjacent to the study. The biomass of these snags was partitioned into the following size classes: 1-hour, 10-hour and 100-hour. The mean biomass of dead sagebrush plants was then used in conjunction with the density of dead sagebrush to determine total standing dead sagebrush biomass. Total aboveground biomass was then calculated as the sum of all grass/herb, dead and downed woody, standing live sagebrush, and standing dead sagebrush fuels (i.e., 13 distinct categories). Additionally, loading of fine fuels was calculated as the total aboveground biomass of all herbaceous materials and sagebrush foliage combined. Although these fuels are technically 1-hr fuels, this fuel category is important in affecting fire behavior and rate of spread as a result of its high surface to volume ratio (Albini 1976, Burgan 1987), and was thus totalled separately.

Postfire herbaceous fuels were determined by clipping ten 30 x 60 cm plots along the opposite side of the preburn herbaceous fuel transect where the prefire fuels were measured. Postfire woody fuels were estimated in each unit by collecting all material in four randomly located 2 x 2 m plots. Fuel consumption was then calculated through subtraction of postfire fuel loads from prefire loads.

To estimate moisture content, six samples of soil (0-2 cm depth), herbaceous fuels, 10-hr downed woody debris, and sagebrush foliage were collected and placed in air-tight containers immediately prior to ignition of each treatment unit. In the laboratory, the samples were weighed, oven dried

for 48 hours at 70°C, and then re-weighed to determine soil and fuel moisture content on a dry-weight basis. Weather conditions were monitored prior to ignition and every 30 minutes during burning. The conditions monitored included ambient temperature, relative humidity, and in-stand (2 m above ground) windspeed.

Each unit was ignited using a drip torch, in a strip-head firing pattern, with strip widths of 5-10 m. Fire behavior data recorded included flame length (m), flame height (m), flame depth (m), flame angle (degrees off the horizontal), rate of spread (m/s), and residence time of active flaming combustion(s) (Alexander 1982). All of the above fire behavior characteristics were measured by randomly selecting 5 to 12 areas in each unit for observation. Photographs taken of the flames at selected observation points were used to verify accuracy of ocular estimates of flame dimensions.

From the measurements of flame length (FL), the rate of energy release per meter width of flame front, or fireline intensity (I_{FL}) was estimated. Fireline intensity was calculated utilizing the empirical equation developed by Byram (1959), and given in Rothermel and Deeming (1980):

$$I_{FL} = 258*FL^{2.17} \quad [kW/m]$$

Reaction intensity (I_R), or the rate of energy release per square meter of flaming zone, was calculated by dividing the fireline intensity by flame depth (Albini 1976, Alexander 1982). The total energy released in the active flame front, or heat-per-unit-area (H_a), was calculated by dividing the fireline intensity by the rate of spread (Rothermel and Deeming 1980). The total heat load released by the fire was calculated as the product of the total fuel consumed and the net heat of combustion of that fuel. No values for heat of combustion of sagebrush fuels could be found in the literature. Therefore, we utilized an average value for wood fuels given by Van Wagner (1972). A value of 18,700 kJ of energy released per kg of fuel consumed and a reduction of 24 kJ per moisture percentage point of the fuels were used in this calculation. Considering the high quantities of volatile oils and waxes found in big sagebrush foliage, this energy estimate is believed to be conservative.

Analysis of all variables employed the use of a paired t-test to test for differences between burn treatment means. Tests of significance were conducted at the p = .05 level, using a two-tailed probability.

Results and Discussion

Aboveground Biomass of Sagebrush Dominated Ecosystems

Total aboveground biomass ranged from 5 to 12 Mg/ha in the nine experimental units; fall treatment units averaged 10.59 Mg/ha, as compared to 6.23 Mg/ha in the spring treatments (Table 1). Much of this disparity between treatments was due to greater amounts of live sagebrush in the fall units. Mean sagebrush canopy cover was 15 percent in fall units and 7.5 percent in spring units. Consequently, all fuel categories associated with the live sagebrush were different between treatments (Table 1). The proportion of the total aboveground biomass consisting of live sagebrush was accordingly relatively higher in the fall units (48 percent) as compared in the spring units (29 percent).

TABLE 1. Aboveground biomass (Mg/ha) of basin big sagebrush ecosystems at the John Day Fossil Beds National Monument, Oregon. Data correspond to spring and fall prescribed burn units. Numbers in parentheses are the standard error of the group mean.

Fuel Category	Treatment	
	Fall	Spring
Live Sagebrush		
Attached Dead*	1.06 (.12)	0.42 (.16)
Total Live*	4.11 (.48)	1.67 (.63)
Foliage*	0.84 (.13)	0.32 (.12)
1-hour T.L.*	1.16 (.19)	0.44 (.16)
10-hour T.L.*	1.35 (.22)	0.52 (.19)
100-hour T.L.*	2.18 (.25)	0.89 (.33)
Standing Dead Sagebrush		
1-hour T.L.	0.11 (.02)	0.11 (.02)
10-hour T.L.	0.28 (0.6)	0.26 (.04)
100-hour T.L.	0.50 (.11)	0.46 (.07)
Grass/Herbs		
Live*	0.00 (0)	0.86 (.22)
Dead	3.01 (.65)	1.81 (.22)
Dead and Downed Wood Debris		
1-hour T.L.	0.52 (.24)	0.31 (.09)
10-hour T.L.	0.58 (.21)	0.25 (.13)
100-hour T.L.	0.04 (.04)	0.00 (0)
Totals		
Standing Live*	4.11 (.48)	1.67 (.63)
Standing Dead*	1.96 (.19)	1.26 (.09)
Grass/Herbs	3.01 (.65)	2.67 (.23)
1-hour T.L.*	1.80 (.36)	0.86 (.11)
10-hour T.L.*	2.22 (.37)	1.03 (.20)
100-hour T.L.*	2.72 (.24)	1.35 (.28)
*Total Aboveground Biomass**	10.59 (1.12)	6.23 (.69)

*Denotes significant difference between treatments ($p < .05$).

There were no significant differences between treatment units in terms of standing dead woody debris, dead and downed woody debris, or total grass/herb fuels (Table 1). The total biomass of fuels from the live sagebrush component was greater in the fall treatment units, averaging 4.11 Mg/ha, compared to a mean of 1.67 Mg/ha in spring units. Similarly, total standing dead woody debris (i.e., the attached dead on live shrubs plus dead shrubs) was greater in the fall units (1.96 Mg/ha), than in the spring units (1.26 Mg/ha). Herbaceous fuels averaged 3.01 Mg/ha in fall units and 2.67 Mg/ha in spring units. As expected, the spring units contained greater amounts of live grass/herb fuels, a direct result of the inherent phenological differences that result from burning in different seasons. The mass of herbaceous fuels in both burn treatments exceeds the minimum threshold values for fire spread. Beardall and Sylvester (1976) estimated that 674-786 kg/ha is required to sustain fire spread; thus the loads here are roughly four times that required for sustained combustion.

In both treatments, the relative distribution of biomass among the fuel size-classes was similar. The largest proportion of biomass was in the fine fuels, comprising 37 percent of the total aboveground biomass in fall units and 48 percent in spring units. The next most abundant fuel class was 100-hr woody debris, comprising from 23-28 percent of the total fuel load. The 1-hr fuels comprised 13-17 percent of total aboveground biomass, and 10-hr fuels comprised 16-21 percent of the total aboveground biomass.

Fuel Moisture and Fire Weather

Soils and 10-hr fuels were very dry (3-9 percent moisture content) during both fires, and no differences between treatment units were detected. However, there were differences between spring and fall treatment units in regard to the moisture content of fuels (Table 2). There was no measurable quantity of green herbaceous material on fall units because all grass/herb biomass had completely cured by the time of burning, averaging 8.9 percent moisture content. In contrast, approximately 30 percent of the grass/herb biomass was green and living in the spring burn units. These fuels averaged 143 percent moisture content. Thus, the effective moisture content for the herbaceous fuel layer was significantly higher in the spring burn units.

TABLE 2. Environmental conditions associated with fall and spring prescribed burns conducted at the John Day Fossil Beds National Monument, Oregon. Data include date and time of prescribed burns, ranges of weather conditions, and fuel moisture contents (n = 16 samples per treatment). Numbers in parentheses are the standard error of the group mean.

Treatment	Fall	Spring
Date	9/25/87	5/24/88
Time of burning	9:35-13:45	12:35-15:26
Temperature (°C)	15-18	23-35
Relative Humidity (%)	41-48	21-24
Windspeed (kph)	0-15	0-17
Moisture Content (%)		
Soil surface	2.90 (.20)	3.21 (.41)
Dead grass/herb	8.88 (.66)	7.36 (.87)
Live grass	--*	142.60 (11.79)
Sagebrush foliage**	97.19 (6.27)	186.02 (5.12)
10-hr Timelag	4.59 (.09)	4.99 (.35)

*Not sampled due to lack of material.
**Denotes a significant difference between treatment means ($p < .05$).

Another striking difference in fuel moisture was in the sagebrush foliage. Sagebrush foliar moisture levels were 186 percent in spring burns, compared to 97 percent during fall burns. This difference is most likely due to the phenological changes in big sagebrush. During spring, when soil moisture is relatively available, high rates of stomatal conductance and photosynthesis occurs in sagebrush (Depuit and Caldwell 1973). These higher moisture levels in live fuels may be responsible for the somewhat lower consumption rates, lower levels of fireline intensity, and other parameters of fire behavior that were observed during the spring burns.

Moisture content of dead herbaceous materials were similar in both treatments, although marginally drier in the spring units. This is likely a reflection of the lower relative humidity during the spring burns (Table 2). However, the effect of the lower relative humidity and higher ambient temperatures on fire behavior and consumption apparently was overshadowed by the presence of a substantial quantity of live fuels at much higher moisture contents in the spring burns.

Fire Behavior

The differences in aboveground biomass and fuel moisture content resulted in highly significant differences in fire behavior (Table 3). Flame lengths

in the fall treatment averaged over 4 m compared to less than 2 m in the spring burn. As fireline intensity (I_{FL}) varies exponentially with flame length, this difference resulted in greater than a seven-fold difference in fireline intensity. Likewise, the rate of spread of the flame front was six times faster in the fall burn, even though temperature was lower and relative humidities were higher than in the spring burns.

TABLE 3. Fire behavior characteristics and fuel consumption for fall and spring prescribed burn treatments. Numbers in parentheses are the standard error of the group mean.

Variable	Treatment	
	Fall	Spring
Flame length* (m)	4.14 (0.77)	1.74 (0.77)
Intensity (I_{FL})* (kW/m)	6,441 (1,861)	883 (100)
Intensity (I_R) (kW/m^2)	591 (169)	346 (42)
Flame Height* (m)	2.17 (0.31)	1.12 (0.02)
Flame Depth* (m)	10.35 (1.84)	2.56 (0.21)
Rate of Spread* (m/s)	1.57 (0.29)	0.23 (0.03)
Heat per Area (kJ/m^2)	3,253 (812)	3,935 (461)
Total Energy* (kJ/m^2)	18,119 (2,357)	9,267 (1,464)
Residence Time (s)	6.92 (0.91)	11.66 (6.92)
Consumption* (Mg/ha)	9.80 (1.30)	5.23 (0.91)

*Denotes a significant difference between treatment means ($p < .05$).

The reaction intensity and heat-per-unit-area were approximately equivalent in both treatments (Table 3). The linear advance of the flame front (i.e., the rate of spread) was only 0.23 m/s in spring burns compared to 1.57 m/s in the fall treatment. In addition, the residence time of the active flaming zone was roughly twice as long in the spring burns. The slower rate of spread and longer residence time in spring burns was most likely related to the higher moisture content of the live fuels during the spring burn. The average wind/slope factors which would also affect rate of spread were roughly the same in both treatments.

The fall burns released twice as much total energy as the spring burns (i.e., 18,119 kJ/m^2 and 9,267/kJm^2). In contrast heat per unit area (H_a) was approximately equivalent for the two treatments. This reveals a shortcoming of using heat-per-unit-area to assess fire effects. H_a reflects only the heat flux realized in the active flame front. Therefore, this value differs from the total energy released in the same way as the amount of fuel consumed in the active combustion zone differs from the total fuel consumed. Photographs revealed that a considerable standing mass of woody debris remained immediately after the passage of the fire front, although the majority of these fuels were consumed during the smoldering phases of combustion. Fuels consumed after the passage of the flame front continue to release heat, and may be extremely important in regard to the effect of sustained high temperatures on living tissues (Wright 1971). The two-fold difference in total energy release may be reflected in terms of effects on plants, as well as below ground heat flux (Sapsis 1990). Consequently, total energy release may prove in this instance to be a better parameter for correlation with fire effects than heat-per-unit-area.

We interpret differences in flame behavior to be largely a manifestation of differences in fine fuel moisture. With fine fuel loads roughly equivalent, and actually more severe fire weather occurring during the spring burn, the dampening effect of higher fuel moisture in the spring appears to be the most logical factor contributing to the marked differences in active flame parameters. In contrast, total energy release is proportional to fuel consumption, and differences seem more likely to simply be the result of differences in fuel availability.

Fuel Consumption

Total biomass consumption by fire was significantly different between the two treatments, with roughly twice the consumption in the fall (9.80 Mg/ha) as in the spring (5.23 Mg/ha) (Table 4). This difference in consumption is a reflection of both the differences in total fuels loads, and in the total quantity of fuels available for combustion (a reflection of significant differences in fuel moisture). However, since postfire aboveground biomass (residual fuels) was not significantly different (Table 4), moisture content did not appear to markedly affect consumption. Despite large differences in moisture content, fuel consumption of the fine fuels was not different between treatments. However, consumption of both 10-hr and 100-hr fuels was significantly greater in the fall units, apparently more a result of greater loads than moisture status.

In terms of total biomass consumption on a percent basis, the fall treatment averaged 93 percent consumption, as compared to 84 percent in the spring burns. Fine fuels and 100-hr fuels were

TABLE 4. Residual fuel loads and fuel consumption (Mg/ha and %) for fall and spring prescribed burns. Numbers in parentheses are the standard error of the group means.

RESIDUAL FUEL LOADS:	Treatment	
Fuel Category	Fall	Spring
Fine Fuels	0.23 (.16)	0.23 (.03)
1-hr T.L.	0.15 (.04)	0.20 (.05)
10-hr T.L.	0.32 (.02)	0.49 (.07)
100-hr T.L.	0.09 (.04)	0.08 (.03)
Total Biomass	0.79 (.18)	1.00 (.22)
FUEL CONSUMPTION:		
Fuel Category	Fall	Spring
Fine Fuels (Mg/ha)	3.64 (.72)	2.76 (.27)
percent	94.54	92.31
1-hr T.L. (Mg/ha)	1.65 (.40)	0.66 (.16)
percent	91.66	76.74
10-hr T.L.* (Mg/ha)	1.90 (.39)	0.54 (.27)
percent	85.59	52.43
100-hr T.L.* (Mg/ha)	2.63 (.28)	1.27 (.31)
percent	96.69	94.07
TOTAL* (Mg/ha)	9.80 (1.30)	5.23 (.91)
percent	92.54	83.95

*Denotes a significant difference between treatment means ($p < .05$).

consumed at similar levels in both treatments, ranging from 92-96 percent. The 1 and 10-hr fuels were consumed at lower percentages in the spring units. Thus, most fuels were consumed, despite differences in fuel moisture.

The potential misrepresentation of fire effects through reporting only consumption in terms of percent of prefire fuel loads is apparent through examination of Tables 1 and 4. In this situation, where prefire fuels were significantly different between treatments, it would be misleading to only report that biomass consumption varied by less than 10 percent. Consequently, it seems appropriate that both gross consumption and consumption as a percent of prefire fuel loads be expressed when evaluating fire effects.

Table 4 reveals an anomaly associated with the consumption of the 10-hr fuel size-class. While all other fuel categories demonstrated rather similar consumption percentage rates, there was a striking difference between treatments with respect to 10-hr fuel consumption. Where almost 85 percent of the 10-hr fuels were consumed by the fall fire, only 52 percent of the 10-hr fuels were consumed by the spring burn. It seems probable that higher moisture content of live 10-hr fuels in the spring units contributed to the lower consumption recorded.

Conclusion

Fires in sagebrush ecosystems are clearly variable, both in terms of fuel consumption and fire behavior. Variability is likely to result from differences in fuel characteristics, weather, and topography. Since weather and topographic features were roughly equivalent in the two fire treatments recorded here, it appears likely that differences in fuel characteristics are largely responsible for observed differences in these two treatments. Specifically, rates of fuel consumption (i.e., consumption percent) were high in both burns, despite differences in total loads and moisture content. Thus, as fuel loads increase, we would expect commensurate increases in total consumption (and total energy release), somewhat independent of fuel moisture. In contrast, fire behavior associated with the active flame front seems highly sensitive to fuel moisture. This is evident by the fact that despite the two treatments being equivalent in fine fuel loads, fire behavior was dramatically different.

The two fire treatments in this study provide a good contrast of the variability possible in microclimate, fuel moisture, and fuel loads. This is further reflected in differences in fire behavior and fuel consumption, supporting the contention of the inherent variability of fire in space and time. The dramatic differences in fire behavior and biomass consumption underscore the need of quantification of these ecosystem parameters prior to, during, and following the fires. These data could then provide a basis for understanding the natural role of fire, as well as its potential uses as a land management tool.

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Factors Influencing the Scarification and Germination of Three Montane Sierra Nevada Shrubs

Abstract

Following fires in the forested ecosystems of the northern Sierra Nevada and southern Cascade mountains, early successional communities are often dominated by shrubs that arise from seeds that have remained viable in soil seedbanks for decades, or even centuries. The germination response of seeds of three seral montane shrub species was investigated following exposure to differing types of heat (wet vs. dry), temperature levels, durations of temperature exposure, and differing lengths of stratification periods. The highest germination (>60%) of *Ceanothus integerrimus* H. & A. was observed for seeds scarified by a wet-heat (treatment) of 75-100°C for 4-8 minutes. Wet-heat treatments were more effective than dry-heat treatments in scarifying seeds at all temperatures below 100°C. At dry-heat exposures for 120°C, 68-81% of the seeds were killed. Germination was less than 2% for seeds that were not exposed to any heat (scarification) treatment. Similarly, without stratification following scarification, germination was ≤5%. However, germination of scarified seeds followed by a stratification treatment was as high as 81.3%. No significant germination was found for seeds of *Arctostaphylos viscida* Parry or for *Arctostaphylos mewukka* Merriam regardless of treatment. Seeds of these species require another chemical, physical, or environmental factor in order to break embryo dormancy or they may have inherently low germination rates.

Introduction

In the ponderosa pine (*Pinus ponderosa* Dougl. ex P & C Lawson) and mixed conifer-dominated ecosystems of North America, early successional stages are often dominated by shrub species that originate from seeds stored in soil seedbanks. These seeds are deposited in the early stages of the sere prior to conifer dominance. During periods of conifer dominance, they may remain dormant, yet viable in extremely high numbers until dormancy is broken by fire or some other disturbance. Approximately 5 million viable seeds/ha of *Ceanothus* and *Arctostaphylos* spp. were found in the soils of an 80-100 year old mixed conifer stand in California (Anderson 1985).

Following fire or some other disturbance, these seeds germinate in numbers that far exceed the carrying capacity of the site (Wells 1969, Weatherspoon 1988, Kauffman 1987). However, fire severity (i.e., levels of biomass consumption and hence heat flux into the soils) has been shown to have dramatic influences on postfire shrub seedling density. For example, Weatherspoon (1988) found that the soil seedbank of *Ceanothus velutinus* Dougl. ex Hook. (snowbrush ceanothus) was not significantly reduced by prescribed understory burns of moderate or low consumption but up to 94% were destroyed by high consumption fires. Similarly, Kauffman (1987) found a strong relationship between fuel consumption and *Ceanothus integerrimus* H. & A. (deerbrush) density. Seedling densities of this species were 216,000/ha following prescribed understory fires of high consumption (92% consumption of dead and downed fuels), and 1667/ha in understory burns of moderate consumption (58% fuel consumption). Apparently, in the high consumption burn, soil heat flux was adequate to scarify large numbers of seeds. In contrast, the lower heat flux from the moderate consumption burn did not influence large numbers of the soil seedbank.

In recently disturbed sites (e.g., following clearcut logging), surface soil temperatures exceeding 60°C are possible on hot summer days. The exposure of the soil seedbank to these temperatures has been reported to be adequate for scarification and subsequent germination (Christensen and Muller 1975, Gratkowski 1962).

Shrubs of the *Arctostaphylos* and *Ceanothus* genera serve an important function in forest ecosystems. These species provide habitat and forage for mammals and birds (Cronemiller 1959). Many *Ceanothus* species have nitrogen fixing capabilities that result in the replacement of nitrogen volatilized by the fire (Binkley *et al.* 1982, Youngberg and Wollum 1976). *Ceanothus* and *Arctostaphylos* spp. also serve as intermediate hosts of mycorrhizal fungi which can have important

symbiotic relationships with conifers (Perry *et al.* 1987). Finally, they can be significant competitors with regenerating conifers in forest plantations (Conard and Radosevich 1982).

Because of the economic and ecological importance of these species, it is essential to understand the factors affecting the dynamic relationships between fire or other forest disturbances and the germination of these shrubs. Through increased understanding of these relationships, it may be possible to efficiently manipulate the abundance of these species (i.e., decrease their abundance where they are not desired or conversely, increase their abundance where they are desired). To better understand these relationships, a laboratory germination study of three montane shrub species was conducted to investigate: (1) The relationship of seed germination with varying levels and durations of temperature exposure; (2) The influences of wet versus dry-heat environment on germination; (3) The influences of stratification length on germination.

Methods

Seeds of three montane chaparral species were used in this study: *Ceanothus integerrimus* var. *californicus* (Kell.), (deerbrush ceanothus), *Arctostaphylos viscida* Parry (whiteleaf manzanita) and *arctostaphylos mewukka* Merriam (Indian manzanita). These species are common early successional constituents of mixed conifer ecosystems in the northern Sierra Nevada. Although these species have been observed to have some capacity to sprout following crown mortality (Kauffman and Martin 1990), their primary mode of regeneration following disturbance is through seed germination.

Seeds were hand collected at the time of ripening (August-September, 1983 for *C. integerrimus* and *A. viscida*, and August, 1984 for *A. mewukka*). *C. integerrimus* and *A. viscida* were collected from two early seral, shrub-dominated communities located on the Quincy Ranger District, Plumas National Forest and the Challenge Experimental Forest (also a part of the Plumas National Forest). *A. mewukka* was collected at the Challenge Experimental Forest. Elevation of these sites ranged from 1000-1350 m and mean annual precipitation ranged from 800-1800 mm.

For each species, seeds were collected from at least 25 randomly selected shrubs. After collection, seeds from all shrubs and locations were thoroughly mixed together. Lots for the germination experiments were selected from these composite samples. A sample of seeds of each species was judged for viability by a cutting test similar to that of Young *et al.* (1978). During the formation of all seed lots, criteria for the judgement of viability included seeds free of insect and mechanical damage, and of a proper shape and seedcoat texture. If shriveled, damaged or pale in color, the seed was rejected for germination. Heat treatments were applied in December, 1984. Germination trials occurred from February-May 1985.

Experiment 1. Seed Responses to Varying Temperatures and Duration of Exposure

The scarification and germination response to 24 different treatment combinations was examined in this study. As in all experiments in this paper, each treatment consisted of 3 replicates (lots) of 50 seeds each. Approximately one-half of the treatments consisted of a "wet heat" exposure and one-half consisted of a "dry heat" exposure. In the "wet heat" treatments, each seed lot was exposed to a given temperature level for a given period of time by submersion in a water bath. An oven with a modified door for rapid insertion of the seeds with minimal heat loss was utilized for the "dry heat" treatments. The temperature levels for both heat treatments included: 45°, 60°, 75°, 90°, and 100°C. In addition, a 120°C dry treatment and a control (no heat) treatment was established.

Seeds were exposed to each temperature level for 4 and 8 minutes with the exception of the 60° treatments where only a 4 min. exposure was implemented. For *C. integerrimus* and *A. viscida* at the 90° temperature level, and additional treatment with an exposure duration of 16 minutes was also examined. Following temperature exposure, all seeds were stratified by packing them in moist perlite and placing them in a cooler at 3°C for 60 days.

An additional treatment for *A. mewukka* was examined; the effect of animal digestion on seed germination. Coyote (*Canis latrans*) feces containing large amounts of *A. mewukka* seeds were collected. These samples were collected at the same sites and times as the fresh seeds. These seeds were also exposed to temperatures of 75° and 100° for 4 minutes. A control (no heat) treatment was also examined.

Experiment 2. The Effect of Stratification Length on Germination

A total of 16 treatment combinations were examined in this experiment. Seeds were exposed to wet or dry heat treatment of 90°C for a duration of 4 and 8 min. Utilizing these scarification combinations, four stratification treatments were examined: (1) 60 days stratification following scarification, (2) 90 days stratification following scarification, (3) 60 days stratification and then scarification, and (4) no stratification. Stratification temperature was 3°C for all treatments.

For the germination trial, each lot of seeds was placed in petri dishes between blotter paper and moistened with distilled water. To prevent waterlogged or dry conditions, a layer of perlite was placed between the blotter paper and the bottom of the petri dish. During germination trials, seeds were kept at a temperature of approximately 21°C, and all were exposed to approximately 11 hours of light daily. Germination was recorded weekly for 5-6 weeks. Emergence of the hypocotyl from the seed coat was the criterion for determination of germination.

During germination trials, the number of *C. integerrimus* seeds that imbibed water (i.e., were scarified) and those that died were recorded to assess the treatment effects on these variables. Mortality was recorded when the seed was obviously rotted. These were easily separated from living seeds which did not become moldy and remained firm. Death and water uptake (imbibition) were not discernible for the *Arctostaphylos* spp.

It was estimated that greater than 95% of the seeds utilized were viable. Data were analyzed utilizing Analysis of Variance. If significant, a multiple comparison test (Student-Newman-Keuls') was utilized to determine significant differences among treatments.

Results and Discussion

Ceanothus integerrimus

Temperature Effects on Scarification and Germination

The highest levels of germination occurred following exposure to the 75°C, 90°C and 100°C treatments (Table 1). In the wet-heat treatments, germination was greatest when seeds were exposed to 90°C for 4 and 8 minutes (73-75% germination), but declined in lots exposed for 16 minutes (46.7%). The highest rate of germination in dry treatments was in lots exposed to 100°C for 4 and 8 minutes (52-53%).

There were large differences in the percent of germination between wet and dry-heat treatments at all temperatures below 100°C (Table 1). For example, germination was greater than 32% for all of the wet-heat treatments below 100°C. In contrast, there was little or no germination in dry heat treatments of 45°C or 60°C. Seed germination was significantly higher in wet treatments over dry treatments at exposures of 60°C, 75°C and 90°C temperature levels (Table 1).

Following exposures of 60°C for four minutes, 100% of seeds exposed to wet heat and 27% of seeds exposed to dry heat were scarified. Germination was 48% and 2% for the wet and dry heat, respectively. This indicates that the environment surrounding the seeds will dramatically influence rates of scarification and hence, germination. Under natural conditions, if surface soil temperatures are ~45-60°C when soils are saturated, thermal scarification from solar insulation is possible. Conversely, when soils are dry, temperatures of 90°C may be required to achieve these same levels of scarification (Table 1).

The percentage of seeds that were scarified was significantly different among seeds exposed to wet or dry heat. In wet-heat treatments, all treatments above 45°C had a 100% level of scarification. In contrast, of all the dry-heat treatments, only exposure to 120°C resulted in 100% scarification (Table 1).

The processs for germination is initiated in *Ceanothus* species when gas and water exchange occurs through the hilar fissure; an opening that bisects the hilum of the seed apex (Gratkowski 1962). In mature dormant *Ceanothus* seeds, the hilar fissure is sealed by opposing pressures of the two edges of this fissure against each other. Heat (scarification) in *Ceanothus* opens the hilar fissure allowing for gas and water exchange to occur between the surrounding environment and the endosperm and embryo of the seed. In studies of *C. velutinus* seeds, Gratkowski (1962) reported that heat affected only the hilum of seeds rendering it permeable to moisture; the rest of the seed coat was not affected and remained impermeable. From examination of scarified *C. integerrimus* seeds, heat appeared to only affect the hilum. After imbibition,

TABLE 1. Percent germination, death, and scarification for *Ceanothus integerrimus* seeds exposed to differing temperatures, lengths of exposure and different heat sources. Stratification period was for 60 days. Data are mean and standard error (in parentheses).

Temperature °C	Duration of Exposure (min)	Heat Source					
		Wet (Water bath)			Dry (Oven)		
		% Germination	% Dead	% Scarification	% Germination	% Dead	% Scarification
Control—no heat treatment		1 (1)	11 (1)	15 (1)	–	–	–
45°	4	33 (7)	17 (5)	69 (8)	3 (1)	13 (3)	25 (5)
	8	33 (15)	5 (1)	86 (3)	1 (1)	14 (2)	25 (1)
60°	4	48 (14)	9 (2)	100 (0)	2 (1)	16 (4)	27 (6)
	8	–	–	–	9 (1)	14 (4)	29 (2)
75°	4	68 (16)	19 (6)	100 (0)	27 (10)	11 (3)	48 (4)
	8	63 (13)	19 (8)	100 (0)	16 (4)	11 (3)	50 (5)
90°	4	75 (7)	23 (5)	100 (0)	23 (12)	13 (2)	70 (34)
	8	73 (4)	19 (6)	100 (0)	36 (14)	15 (2)	72 (5)
	16	47 (5)	28 (11)	100 (0)	27 (11)	12 (5)	68 (9)
100°	4	67 (8)	27 (7)	100 (0)	53 (8)	15 (3)	87 (1)
	8	45 (1)	41 (10)	100 (0)	52 (10)	19 (8)	85 (2)
120°	4	–	–	–	11 (1)	68 (13)	100 (0)
	8	–	–	–	8 (4)	81 (17)	100 (0)

openings along the hilar fissure were apparent with the naked eye. In addition, emergence of the radical always originated through the hilar fissure.

The difference in percent of seeds that were scarified at lower temperatures indicates that exposure to wet-heat is more efficient in opening the hilar fissure than the dry-heat. Whether this was a result of increased thermal conductivity in a water medium or some chemical-mechanical reaction due to contact with water is unknown.

Seed mortality did not significantly differ in all dry-heat treatments from 45-100°C. However, in the 120°C treatments, mortality significantly increased and was over 4 times greater than in the 100°C treatments. There was also a relationship between duration of heat and seed mortality at the 100°C level. For example, in the 100°C wet-heat treatments, mortality following 8 minutes of heat exposure was 14% greater than mortality following 4 minutes of exposure. Similar results were reported by Quick (1959) who found the highest germination of *Ceanothus* spp. occurred when boiled for 5 minutes. Germination declined when boiled for longer periods. Quick and Quick (1961) predicted a 4.2% drop in germination would occur for each minute *C. integerrimus* was immersed in boiling water.

Effects of Varying Durations of Stratification

After scarification, gas exchange at lower temperatures is necessary for seeds to overcome certain biochemical inhibitions to germination. Abscisic acid has been identified in the seeds of several species as an inhibitor of germination and has been found to decrease during chilling periods (Arias *et al.* 1976, Wareing *et al.* 1973). Concomitant with the decrease in abscisic acid, Wareing *et al.* (1973) and Arias *et al.* (1976) reported increases in cytokinins and gibberellins which have been found to promote germination. In this study we found that little or no germination occurred in seeds that were not stratified following scarification nor was there appreciable ($<1\%$) germination in seeds exposed to cold periods prior to scarification (Table 2). In contrast, germination was as high as 81% for scarified seeds with a 90 day stratification (Table 2).

Stratification resulted in highly significant increases in germination. In addition, the sample means were consistently higher in the 90 day stratification treatment in comparison to the 60 day stratification treatment. This is particularly true in the dry-heat treatments where germination rates increased from 22.9 to 54.7% in 4-min treatments and from 36.0 to 52.7% in 8-min treatments

TABLE 2. The percent germination of *Ceanothus integerrimus* resulting from four different stratification treatments. Seeds were exposed to heat treatments of 90°C for 4 or 8 minutes prior to stratification. Data are the mean percent germination and standard error (in parentheses). Different superscripted letters denote a significant difference ($P \leq 0.05$) in means between all treatments.

Treatment	Length of Exposure (min)	Heat Source: Wet (water bath)	Heat Source: dry (Oven)
60 d	4	75^{c} (7)	23^{b} (12)
	8	73^{c} (4)	36^{b} (14)
90 d	4	81^{c} (2)	55^{b} (7)
	8	79^{c} (9)	53^{b} (4)
60 d prior to scarification	4	1^{a} (1)	1^{a} (1)
	8	0^{a} (1)	0^{a} (0)
no stratification	4	1^{a} (1)	1^{a} (1)
	8	5^{a} (4)	1^{a} (1)

(Table 2). In both the 60 day and 90 day stratification treatments exposure of seeds to the wet-heat treatment at 90°C resulted in significantly higher levels of germination than identical exposures to dry-heat treatments.

In mixed conifer ecosystems, hundreds of thousands of shrub seedlings/ha have emerged the first postfire spring (Kauffman 1987). Following fire or other disturbance, rapid germination is a competitive advantage facilitating exploitation of limiting resources. For all of the 60 and 90 day stratification treatments, greater than 90% of the seeds that germinated did so in the first week (Figure 1). From examination of Figure 1, it is apparent that stratification requirements of the response of seeds in this species are only met with cool-moist conditions. This can be evidenced through examination of the response of seeds in

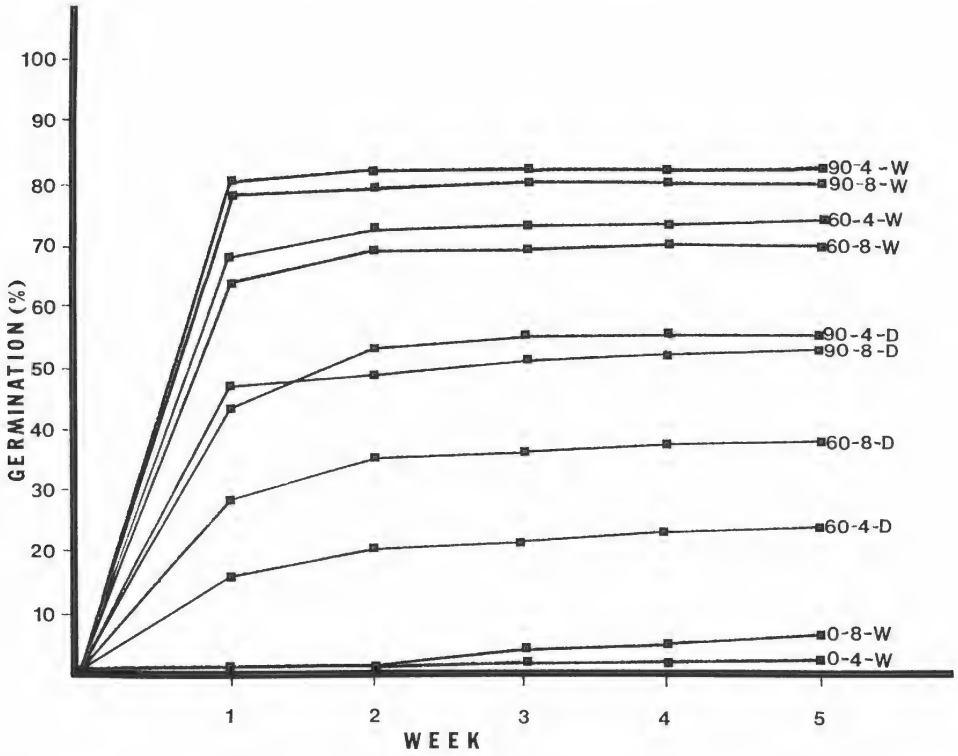

Figure 1. Weekly germination of *C. integerrimus* seeds that were exposed to 90°C for 4 and 8 min. and subjected to 3 different stratification treatments. The first number refers to the length of stratification period (0, 60 or 90 days). The second number refers to the duration of heat exposure (4 or 8 min.). The W refers to the wet heat treatment and the D refers to the dry heat treatment.

TABLE 3. The germination of *Arctostaphylos viscida* and *Arctostaphylos mewukka* following different temperatures and duration of exposure. Numbers are mean and standard error (in parentheses). Stratification length was 60 days. There were no significant differences ($P \leq 0.05$) in germination among treatments.

Treatment	Duration of Exposure (min)	*A. viscida*		*A. mewukka*	
		Wet (Water bath) % Germination	Dry (Oven) % Germination	Wet (Water bath) % Germination	digested/wet+ % Germination
control–no heat treatment		0 (0)	0 (0)	1 (1)	1 (1)
45°	4	0 (0)	0 (0)	4 (2)	–*
	8	1 (1)	1 (1)	0 (0)	–
60°	4	0 (0)	0 (0)	3 (1)	–
75°	4	1 (1)	0 (0)	3 (1)	8 (3)
	8	0 (0)	0 (0)	5 (1)	–
90°	4	0 (0)	1 (1)	5 (3)	–
	8	1 (1)	2 (1)	4 (4)	–
	16	0 (0)	1 (1)	0 (0)	–
100°	4	0 (0)	0 (0)	0 (0)	4 (2)
	8	0 (0)	2 (1)	0 (0)	–

+seeds collected from fresh fecal samples of *Canis latrans*
*–denotes that no trial conducted under this treatment combination

the unstratified treatments that had no increases in germination after exposure to 4-5 weeks of warm-moist conditions (i.e., the later stages of the germination trials).

Response of the *Arctostaphylos* spp.

Regardless of scarification treatment, germination rates were low for both *Arctostaphylos* species (Table 3). There were no significant differences in germination among treatments. The various stratification treatments also resulted in no differences in germination success. For *A. viscida*, the 90°C wet-heat scarification treatment with 60 days of stratification was replicated in 1985 with another seed source. The mean germination of this 1984 seed source was 10.6% ± 1.3. This was significantly greater than the 1983 seed source reported in Table 3. Although germination was significantly different, the percentage of seed viability before scarification treatments was not. However, the seeds collected in 1984 were generally larger in size and mass than the seeds produced the previous year.

None of the various combinations of heat or stratification resulted in high percentages of germination of *A. mewukka* seeds. Although slightly higher than that of fresh seed, germination of seeds found in the feces of coyotes was relatively low ($\leq$8%) (Table 3). Therefore, animal digestion by mammals did not appear to be a significant factor in breaking seed dormancy of this species. However, during the season in which fruits are ripe, large numbers of *Arctostaphylos* seeds are widely dispersed throughout the region via fecal deposition. Thus, it is apparent that consumption of the *Arctostaphylos* fruits by mammals represents an effective means of seed dispersal.

While these species did not respond to these germination treatments, other species of *Arctostaphylos* have been reported to respond to heat treatments (Keeley 1977, Quick 1959). *Arctostaphylos patula* Greene is commonly associated with these species in the mixed conifer zone of the Sierra Nevada. Seeds of *A. patula* were observed to germinate in densities as high as 25,233/ha following fires in the northern Sierra Nevada (Kauffman 1987). Although seedlings of *A. viscida* in densities as high as 1,567/ha were present after fires, their numbers were exponentially less than those of *A. patula* (Kauffman 1987). Although seedling density of *A. viscida* significantly increases following high consumption fires, it is apparent that neither heat nor chemical changes (pH, nutrients, toxins, etc.) in the postfire environment are factors which induce the heavy simultaneous amounts of germination observed for *C. integerrimus* or *A. patula*. Similar results of low germination in laboratory tests of *A. viscida* were reported by Rogers (1949).

Based upon field observations of recently logged sites containing abundant *A. viscida* and *A. mewukka* seedlings, it appears that dormancy is often broken by mechanical scarification of the seed coat. In logged areas, it is frequently observed that *A. viscida* densities are highest where logging equipment has heavily impacted the soil. Areas of impact such as harvested stands in which logging slash has been piled will frequently have higher densities of *A. viscida* than harvested stands in which logging slash was left in place (i.e., areas of less mechanical disturbance). Conversely, logged areas in which slash is left in place and broadcast burned has been observed to have lower densities of *A. viscida* but higher densities of *C. integerrimus.*

Conclusion

The results of this laboratory study aid in the explanation of the mechanisms responsible for the increased densities of *C. integerrimus* in burned areas. Although high densities of *A. viscida* and *A. mewukka* have been observed following anthropogenic disturbances in mixed conifer ecosystems, additional research is needed to determine those physical, chemical, and biological mechanisms responsible for initiating germination.

Seeds of *C. integerrimus* were scarified by heat and required a cool-moist stratification period to break embryo dormancy. Optimum scarification temperatures were 75-100°C. At temperatures less than 100°C with either a 4 or 8 minute period of exposure, wet-heat was significantly more effective at seed scarification and initiation of germination than dry-heat. Seed exposure to a temperature of 120°C for 4 or 8 minutes exponentially increased mortality. Following stratification periods, germination is almost simultaneous with 80-90% of all germination occurring in the first week. In contrast, there was no germination response to thermal scarification by *A. viscida* or *A. mewukka* in this study.

Results of this study would infer that prescribed broadcast burning or wildfires would stimulate germination of *C. integerrimus* but not *A. viscida* or *A. mewukka.* These plant species are important in the ecological functioning of mixed conifer ecosystems and also are of aesthetic and economic significance.

An increased understanding of the germination requirements may allow for successful establishment of these species where desired. Conversely, this information could also aid in controlling densities of these shrubs in situations where unacceptable levels of competition with young conifers in managed plantations exist.

Acknowledgements

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Fire History Along an Elevational Gradient in the Siskiyou Mountains, Oregon

Abstract

Fire history was investigated at two sites in the Siskiyou Mountains of southern Oregon. Kinney Creek in the eastern Siskiyous and Oregon Caves National Monument in the central Siskiyous span an elevational gradient from the Mixed Evergreen zone through the White Fir (*Abies concolor*) zone. The fire frequency of the forest around Kinney Creek, based on fire scars, was about 16 years between 1760 and 1860. Photographic evidence in 1916 of fires from 1854 to 1915 was difficult to corroborate in 1988 based on vegetation evidence. Oregon Caves fire history, reconstructed using a conservative natural fire rotation technique, was 37 years during 1650-1930 for the lower elevation Douglas-fir/oak (*Pseudotsuga menziesii/Lithocarpus-Quercus* spp.) community and 64 years for the highest elevation white fir/herb community, with substantial variation by century. The fire-free interval since 1921 is the longest in more than 300 years. These old-growth forests developed with a much more frequent disturbance history than the wetter, cooler Douglas-fir forests of the Olympic and Cascade Mountains of Washington.

Introduction

The Siskiyou Mountains are within one of the more diverse and complex forest regions of western North America (Whittaker 1960). A wide range of climatic, topographic, and edaphic conditions, and the transitional location of these mountains between diverse regional floras, make the Klamath Region the most central of the forest floras of the West (Whittaker 1960). A complex fire history adds further diversity to the forests of the Siskiyou Mountains.

This study was designed to document fire history along an elevational gradient in the central and eastern Siskiyou Mountains (Figure 1). The Kinney Creek area in the eastern Siskiyous was selected because it was the focus of an earlier study of fire effects (Peterson 1916, Hofmann 1917); it is representative of the lower Mixed Evergreen zone (Franklin and Dyrness 1973). Located at ca. 1200 m elevation, the north aspect of the Kinney Creek study site is a Douglas-fir/Oregon grape (*Pseudotsuga menziesii/Berberis nervosa*) plant association (after Atzet and Wheeler 1984), while the south aspect is a mosaic of Douglas-fir forest, chaparral, and woodland. The Kinney Creek area receives about 90 cm of annual and 13 cm of May-September precipitation (McNabb *et al.* 1982, Froehlich *et al.* 1982).

Oregon Caves National Monument, 20 km to the west in the central Siskiyou Mountains, is a higher elevation (1300-1800 m), higher precipitation site which includes the upper edge of the Mixed Evergreen zone and forest communities characteristic of the White Fir (*Abies concolor*) zone (Franklin and Dyrness 1973). Forest communities

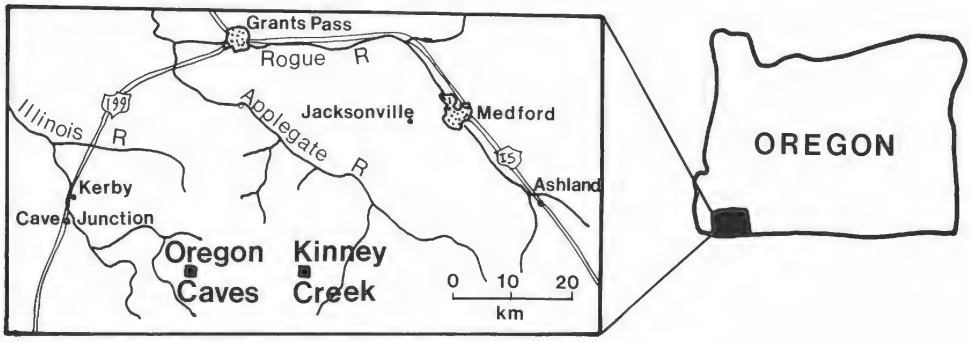

Figure 1. Location of Kinney Creek and Oregon Caves in the Siskiyou Mountains, Oregon.

identified by Agee *et al.* (1990b) include the dry, warm Douglas-fir/oak (*Lithocarpus-Quercus* spp.) community; dry and mesic white fir–Douglas-fir communities; and a white fir/herb community, the coolest and wettest at the monument. Annual precipitation at Oregon Caves is approximately 165 cm, and May-September precipitation averages 16 cm (McNabb *et al.* 1982, Froehlich *et al.* 1982).

Methods

Kinney Creek

Photographic evidence and fire scar records from stumps were used to describe fire history at Kinney Creek. Three locations near Kinney Creek, originally photographed in 1916 (Hofmann 1917), were rephotographed in 1988 from similar camera points. Tree growth since 1916 obscured retakes of some of the original vistas. Increment cores of trees were used to verify dates of fire events identified on the 1916 photographs. On the north-facing slope of Kinney Creek, fire history was reconstructed from scars on 14 stumps over a 2 ha area near the ridgetop. All stumps having fire scars that could be accurately field-counted were included in the sample. This area was logged in 1985 (Richard Marlega, District Ranger, Applegate Ranger District, Rogue River National Forest, personal communication). Annual rings were counted on stumps back to the edges of scarred tissue, and the occurrence year of a fire could then be estimated. A composite fire frequency developed from the stumps in this small area is interpreted as a point frequency.

Oregon Caves

Fire history at Oregon Caves was reconstructed using tree establishment dates as well as fire scars. Tree age data were assembled by placing 50 0.01 ha plots across the 197 ha area, or about 1 per 4 ha. Plots were subjectively chosen to provide uniform spacing and coverage of all forest communities present. On each forested plot, an average of 8 (range 3-24) trees were aged, incorporating the range of size classes on the plot. Samples were cored to the center of the tree and as close to the ground as possible. For each tree sampled, species, diameter at breast and core height, bark thickness, and tree height were recorded. Scars on standing trees were sampled using the increment core technique of Barrett and Arno (1988) whenever possible rather than wedge sampling (Arno and Sneck 1977). Most of the wedge sampling was done on stumps in surrounding Forest Service clearcuts or areas near the boundary of the monument; several wedges were removed from live trees. Samples were returned to the laboratory and sanded. Ages of core or wedge samples were dated using a dissecting microscope.

Dates of tree establishment and fire scars were recorded on topographic maps of the monument and surrounding lands. Fire events, defined either as single fires or a series of fires closely spaced in time, were reconstructed using, in priority order, (a) fire scars from wedge samples, (b) cores extracted to date a fire scar, (c) tree establishment dates, and (d) cores exhibiting aberrant ring patterns associated with dates determined from (a) or (b). Only early seral species (such as Douglas-fir in plant communities of the white fir series, or knobcone pine [*Pinus attenuata*] in plant communities of the Douglas-fir series) were used as evidence of disturbance when tree establishment dates were used to estimate the year of disturbance.

Most of the scar dates were from increment core samples, or stumps adjacent to the monument. Because ring counts on stumps were made in the field, samples were not crossdated and fire events were defined on the basis of scars closely spaced in time together with tree establishment dates from the plots. Accuracy is estimated to be plus or minus: 10 years for samples before 1700, 5 years for samples between 1700-1800, and 2 years for samples after 1800.

Fire events were constructed by first placing dates from fire scars or tree establishment data on the monument map. Fire events previous to 1650 were estimated from individual older trees and scars. Fire events after 1650 were defined under one of the following conditions: two scars evidently of the same time or similar year, 1 scar plus establishment of pioneer tree species, or consistent establishment dates of later seral species (such as white fir) at higher elevation. Single scars not substantiated by other scars or age class evidence were common but were deemed unreliable for indicating the extent of past fire events. Where closely-spaced dates occurred, circles of 250 m radius were drawn around the locations containing each date (Figure 2). The extent of the fire was reconstructed by joining the circles. Circles were not connected if the space between them was larger than a circle diameter, unless the space was more

than 2/3 encircled already. For example, in Figure 2, the area to left center not incorporated in any individual circles is assumed to have burned because that space is essentially surrounded by circles to the left and right. The boundary of the fire was then adjusted slightly in some cases to account for topographic influences on fire behavior: for example, ridgelines were often followed even if the circles slightly overlapped the ridge. Each fire event was separately mapped.

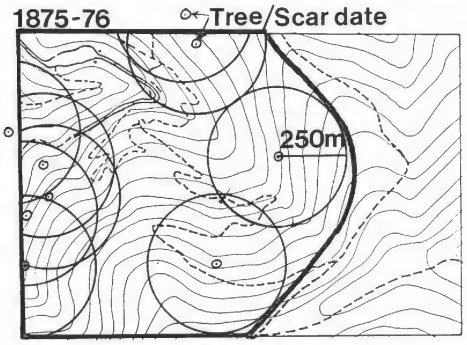

Figure 2. Historic fire extent was reconstructed by locating fire scars or contemporary early seral trees and drawing 250 m radius circles around each point. Fire boundaries were then drawn around those circles, in this case including the western two-thirds of the monument (see Figure 7, 1875-76).

Fire return intervals were calculated using the natural fire rotation (NFR) method (Heinselman 1973). A selected time interval divided by the proportion of the study area burned within that time interval yields the NFR. As applied here, the NFR method produces conservative estimates of fire frequency, because of the need to reconstruct past fire events, some of which may have been erased from the landscape by later fires, and the decision to discard single pieces of evidence. NFR's were calculated by century and by forest community type.

Results

Kinney Creek

The photographic comparison suggests succession has proceeded without perceptible disturbance in most areas since 1916, with edaphically-controlled boundaries remaining stable. The south-facing slope of Kinney Creek in 1916 is shown in Figure 3A, with its 1988 counterpart below (Figure 3B). The boundaries of shallow soil areas (left center) on the far slope are stable over the 70 year period. The texture of the far-distant slope appears similar between 1916 and 1988. There appear to be a few more large trees in 1916 on the east (right) end of the slope, and a few more mature trees to the west (left) in 1988. These are mostly Douglas-fir with some ponderosa pine (*Pinus ponderosa*). The open and brushy portion of the foreground slope is likely the result of an earlier fire. In 1988 (3B) much of this slope is obscured by trees.

Figures 4A-4B show an area slightly upstream from Figures 3A-3B. The Kinney Peak road leaves the Kinney Creek canyon bottom just off the lower right of Figure 4B. In 1916 (Figure 4A) recent fires had burned over the slopes, leaving Douglas-fir residuals along the ridgetops, in the ravines, and along the west-facing (left) slope of the spur ridge in the center of the photograph. By 1988, coniferous forest had regenerated across most of the landscape. In areas that had a mottled texture in 1916, indicating exposed soil and possible periodic slope instability, Pacific madrone (*Arbutus menziesii*) is the current dominant.

The area along Kinney Ridge looking southeast (Figure 5A-5B) has changed markedly since 1916. Prior to the 1916 photograph, this area was repeatedly burned, with numbers on Figure 5A corresponding to fire dates from Hofmann (1917): 1 = 1915; 2 = 1914; 3 = 1910; 4 = 1897; 5 = 1886; and 6 = 1854. Hofmann noted that the repeated burning and complex mosaic of burned and unburned areas made reconstruction of the events very difficult. His map of the burned area (Figure 5C, Peterson [1916]) does not indicate which areas reburned over the 1854-1915 period, although some of the older burns (such as the 1886 burn) are patches separated in 1916 by the more recent burns of 1914 and 1915. Burns closely spaced in time favored those species that can reach maturity quickly with a protected seed bank, such as knobcone pine, which has serotinous cones, or species that sprout (*Quercus* spp., some *Arctostaphylos* spp.).

Hofmann did not indicate how he reconstructed the events of the previous 70 years. The patchiness of such fires in terms of severity complicates reconstruction of fire events based on vegetation present in later decades. A survey of this area in 1988 indicated that Hofmann's chronology would now be very difficult to reconstruct. Three Douglas-firs increment cored in Hofmann's area 5 (at right,

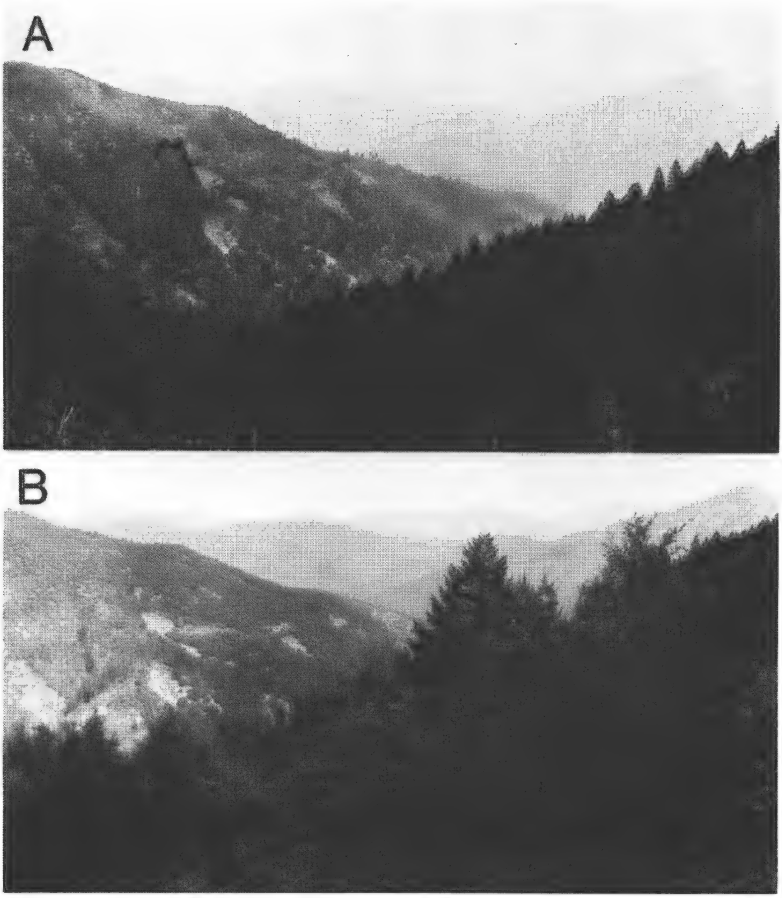

Figure 3. The lower Kinney Creek area in (A) 1916 and (B) 1988, looking northeast from the north aspect of Kinney Creek. Arrow denotes stable boundary of shallow soil area.

Figure 5A-C) yielded estimated dates for germination (which may be 1-3 years in error) of 1889, 1901, and 1905. These dates could be interpreted either as continuous reproduction after the 1886 fire, or regeneration after the 1886 and 1897 fires. A canyon live oak (*Quercus chrysolepis*) cored near the east edge of Area 4 (1897) appeared to have sprouted around 1910, the year of the fire in adjacent Area 3. In area 4 (1897—Figure 5A), two Douglas-firs cored were estimated to have germinated in 1884 and 1899. The 1884 tree must have been missed by the 1897 fire, because at age 13 it likely would have been killed if burned.

On the north aspect of the ridge, immediately out of view to the left of Figure 5A-B and identified by a black dot in Figure 5C, eight fire events since about 1750 were reconstructed based on age class and fire scar data (Table 1). The fire frequency in this 2 ha patch between 1760 and 1860 is about 15 years. Few of the fires identified by Hofmann between 1854 and 1915 burned very far into the mature, north-facing stand of trees, which he identified as "unburned" but which had experienced at least eight fires since the oldest trees had established. The 1915 fire is associated with one Douglas-fir that germinated in 1916 near the crest of the north slope, and Hofmann's 1854 fire may well be the 1856 fire identified by scars; the intermediate fires (1886, 1897, 1910, 1914)

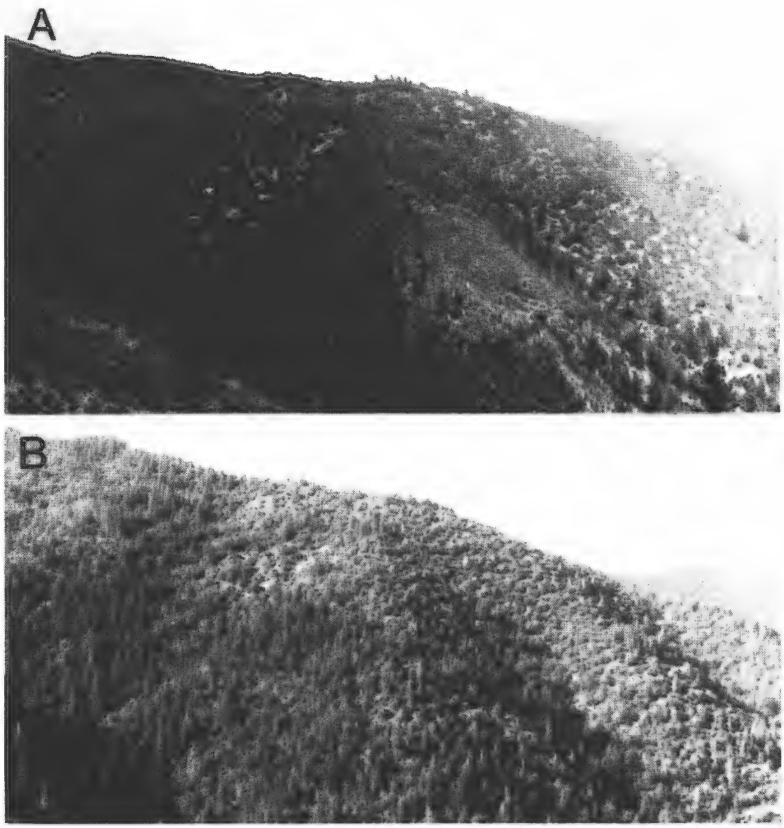

Figure 4. The middle Kinney Creek area in (A) 1916 and (B) 1988. This slope is just above where the present-day road leaves the valley bottom towards Kinney Ridge, and the view looks north.

are all missing from the north aspect set of fire scars, most of which predate the 1850's.

Oregon Caves

The plant communities of this study (Figure 6; Agee *et al.* 1990b) are distributed along a gradient of increasing elevation from northwest to southeast. Lower elevation sites burned more frequently than higher elevation sites (Figure 7).

The oldest detectable fire at Oregon Caves occurred in the 1480's; evidence for this event is very limited. A Douglas-fir stump of that age was found just southeast of the monument in a white fir/gooseberry (*Ribes* spp.) plant association, and a large Port Orford cedar (*Chamaecyparis lawsoniana*) had the oldest of its three fire scars created prior to the early 1500's; this tree probably survived the ca. 1480 fire.

No fire activity was capable of being reconstructed for the 1500's. Evidence of fires that may have occurred has been obscured by subsequent burning. The next fire reconstructed was ca. 1650. Two stump dates from Douglas-fir were found just southeast of the monument boundary. A white fir stump in a riparian area, a sapling-sized tree at the time of the event, showed a significant growth release just after that time, and a Port Orford-cedar along the eastern boundary had a fire scar of that vintage.

Fire evidence becomes more abundant by the end of the 1600's. A fairly widespread age class of Douglas-fir became established along the northern portion of the monument boundary during that

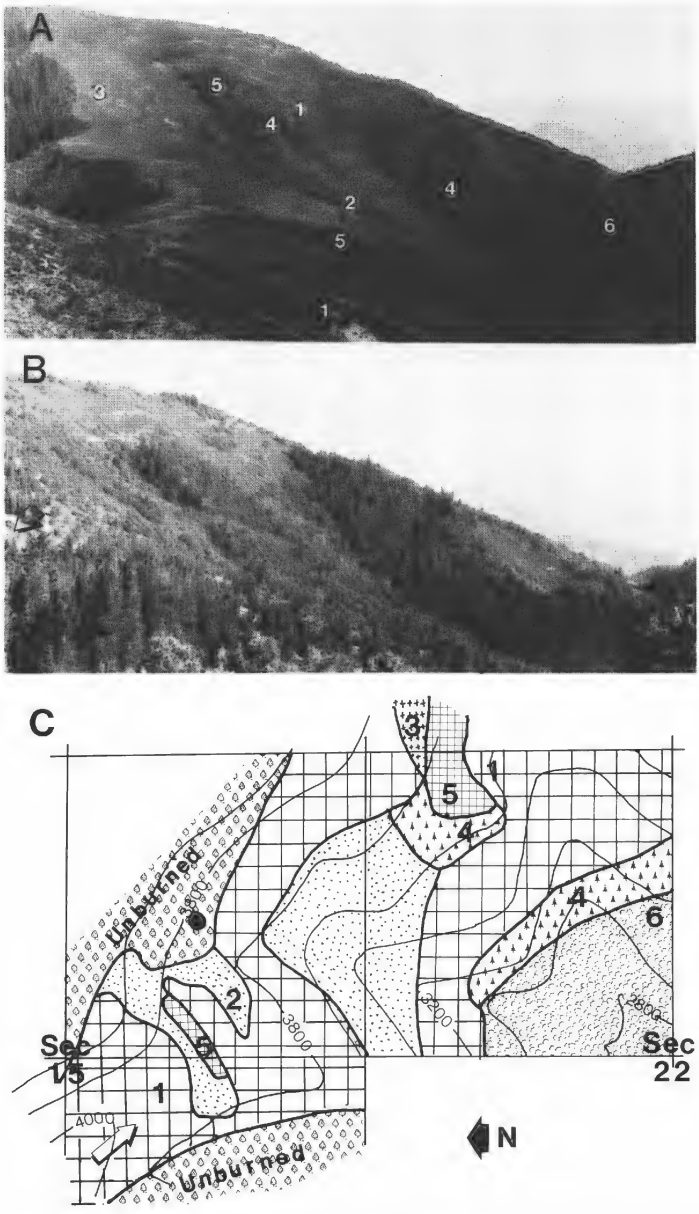

Figure 5. A. The Kinney Ridge area in 1916. The numbers refer to fires identified by Hofmann (1917): 1 = 1915; 2 = 1914; 3 = 1910; 4 = 1897; 5 = 1886; and 6 = 1854. B. The same area in 1988. The arrow at the left is the location of the clearcut stump data shown in Table 1. C. A map of the area redrawn from Hofmann survey (Peterson 1916). The SE 1/4 of Section 15 and NE 1/4 of Section 22, T40S, R4W, is shown, oriented to the line of sight of Figure 5A-B. The numbers represent the general location and same fire years as shown in (A). The black dot near the top is the location of the data in Table 1.

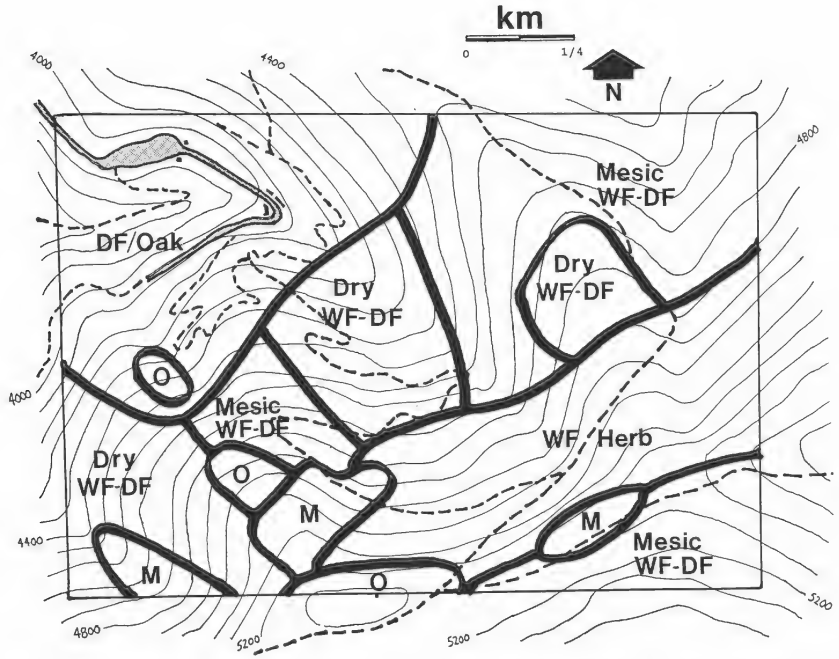

Figure 6. Major plant communities at Oregon Caves, identified with symbols: DF = Douglas-fir; WF = white fir; O = oak; and M = nonforested meadow.

TABLE 1. Estimated fire dates from Kinney Creek clearcut. All trees are Douglas-fir and cut date is assumed to be 1985. Area surveyed was approximately 2 ha.

Tree Number	Scar or Tree Establishment Date(s)								
1		1857	1841	1825	1807	1790?			1747g
2				1825			1780g		
3				1831g					
4		1856					1778		1748g
5			1839						
6						1794		1766g	
7					1807			1773g	
8						1795			
9						1798		1764g	
10			1839			1794			
11				1825					
12								1764g	
13				1825		1797		1765g	
14	1916g								
Estimated Fire Dates*	1915	1856	1839	1825	1807	1795	1778	1763	1746

? = rings not clear

g = estimated germination date

* Estimated fire dates from field counts are subject to some error within a year or two; fire dates estimated from germination dates (column on left and two columns on right) are to be interpreted as the latest date possible (e.g., 1763 might be 1760 or earlier but not 1765).

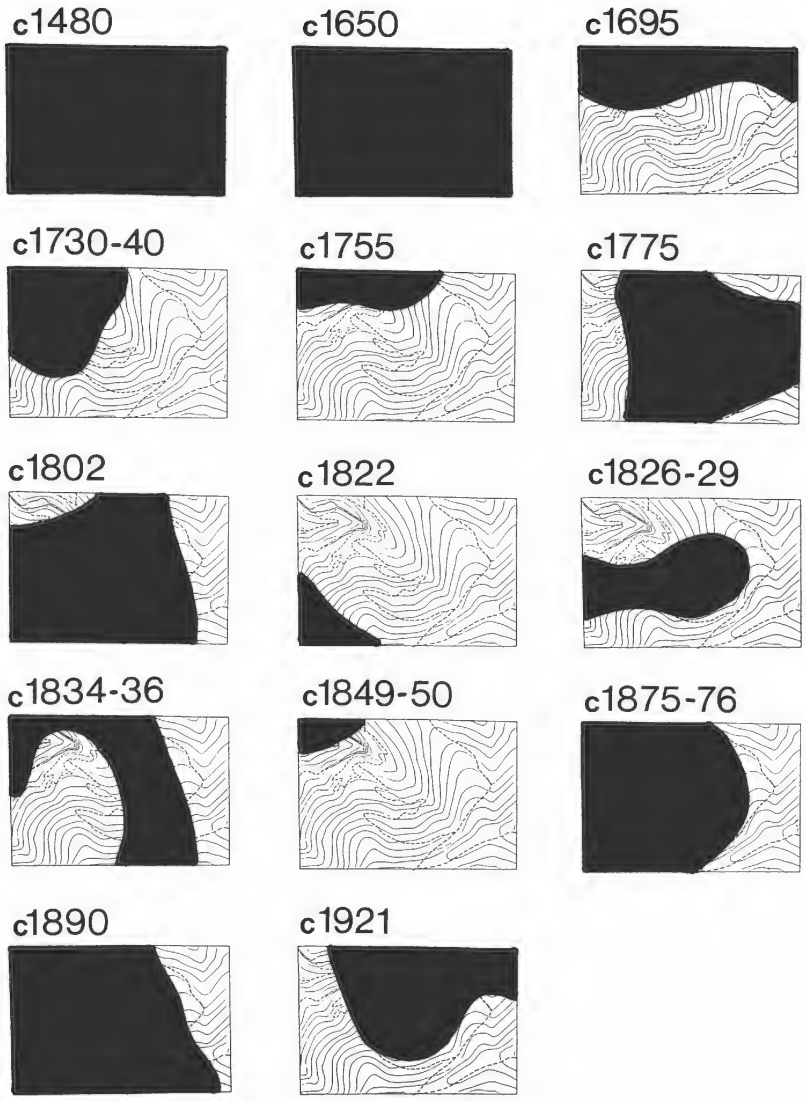

Figure 7. Reconstructed fire events at Oregon Caves since 1480, using the technique presented in Figure 2.

time, suggesting a disturbance date of ca. 1695. This age cohort of Douglas-fir (with germination dates of interspersed trees ranging from 1695 to 1730) suggests one or more moderate to high severity fires; many Douglas-fir became established. Two closely spaced fires seem unlikely due to the lack of any scars on the earliest established members of the cohort. Between 1730 and 1850, at least eight additional fires burned portions of the monument.

Major fires were reported in the vicinities of Kerby and Jacksonville (Figure 1) in the 1865-67 period (Morris 1934) but apparently they did not reach Oregon Caves. In ca. 1875-76, most of the western monument burned. The eastern boundary of this fire is similar to fires in 1802, 1826-29,

and 1834-36. Along the central western edge of the monument, this was a high severity fire. In ca. 1890, another fire burned almost the same area, but was of low severity across much of the monument, leaving occasional scars but not killing many of the young trees that regenerated after the ca. 1875-76 event.

The last significant fire event identified from scars at Oregon Caves occurred in 1921. No administrative records have been uncovered that substantiate this event, but it occurred at a time of frequent burning (Hofmann 1917) and apparently was a low severity underburn within the monument. Since 1921, no major fires have started within or entered the monument. This 70 year period has been the longest fire-free period in more than 300 years.

Fire return intervals (Tables 2, 3) show that fire has not been a spatially or temporally uniform process. The temporal record is biased in that earlier fires of low severity or spatial extent were probably missed. The 16th century is the only century of the last six that fire activity was apparently absent. The increase in fire activity in the nineteenth century may reflect the ability to more accurately identify more recent fires, although the Kinney Creek history suggests that even late nineteenth century fires may be difficult to reconstruct in the Mixed Evergreen zone.

The lower elevation boundary of the white fir/herb type at Oregon Caves appears to have acted as a barrier to fire spread for many fires. Douglas-fir is not common in this type, comprising only 3 percent of the average 72 m^2ha^{-1} basal area. The herbaceous cover may exceed 100 percent during the summer, and the high foliar moisture of the green herbage may retard the spread of surface fires until the herbs cure in late summer. The presence of an all-aged white fir forest (Figure 8), the presence of numerous windthrow mounds, and the absence of Douglas-fir suggest that small scale wind disturbances have encouraged gap-phase reproduction of white fir.

TABLE 2. Natural fire rotation for Oregon Caves by century.

Time Period	Area Burned (ha)	Proportion (p)	Natural Fire Rotation (years)
1400-1500	197	1.0	100
1500-1600	0	0	–
1600-1700	244	1.24	81
1700-1800	213	1.08	93
1800-1900	576	2.92	34
1900-1989	86	0.44	204
1480-1989	1317	6.68	76

TABLE 3. Natural fire rotation for major community types at Oregon Caves, 1650-1930.

Community Type	Area in Type (ha)	Natural Fire Rotation (years)
Douglas-fir/oak	45.1	37
Dry white fir/ Douglas-fir	42.0	43
Mesic white fir/ Douglas-fir	55.4	61
White fir/herb	35.9	64

The mesic white fir/Douglas-fir type has substantially more Douglas-fir: 45 percent of the average 61 m^2ha^{-1} basal area is Douglas-fir. This type had slightly more frequent fire than the white fir-herb type. These two mesic types have the highest numbers of older trees (Figure 8), and historical fires of the last several centuries have typically been of low to moderate severity. The dry white fir/Douglas-fir type, with Douglas-fir comprising 63 percent of the 49 m^2ha^{-1} basal area, has burned more frequently, and surviving trees from earlier fires are more sparse. Most of the trees are younger than the 1875-76 event.

Discussion

When modern forest management developed in the United States, one of the major factors stimulating legislation and policy was the threat of wildfire, particularly large events in the Pacific Northwest in 1902 and 1910 (Pyne 1982). Fire in the forest was characterized as the antithesis of forest management (Agee 1989), and southern Oregon was a center of Forest Service efforts to oppose the use of fire in the forest. Peterson (1916) claimed that local communities opposed fire prevention because of a misunderstanding of the "conservation ideas." He noted that stockmen thought range carrying capacity had declined in the few years that fire protection had been in place. Hofmann (1917) implied in his Kinney Creek study that fires were a product of modern human activity. Haefner (1917) claimed burning by Indians, miners, stockmen, and hunters in the late

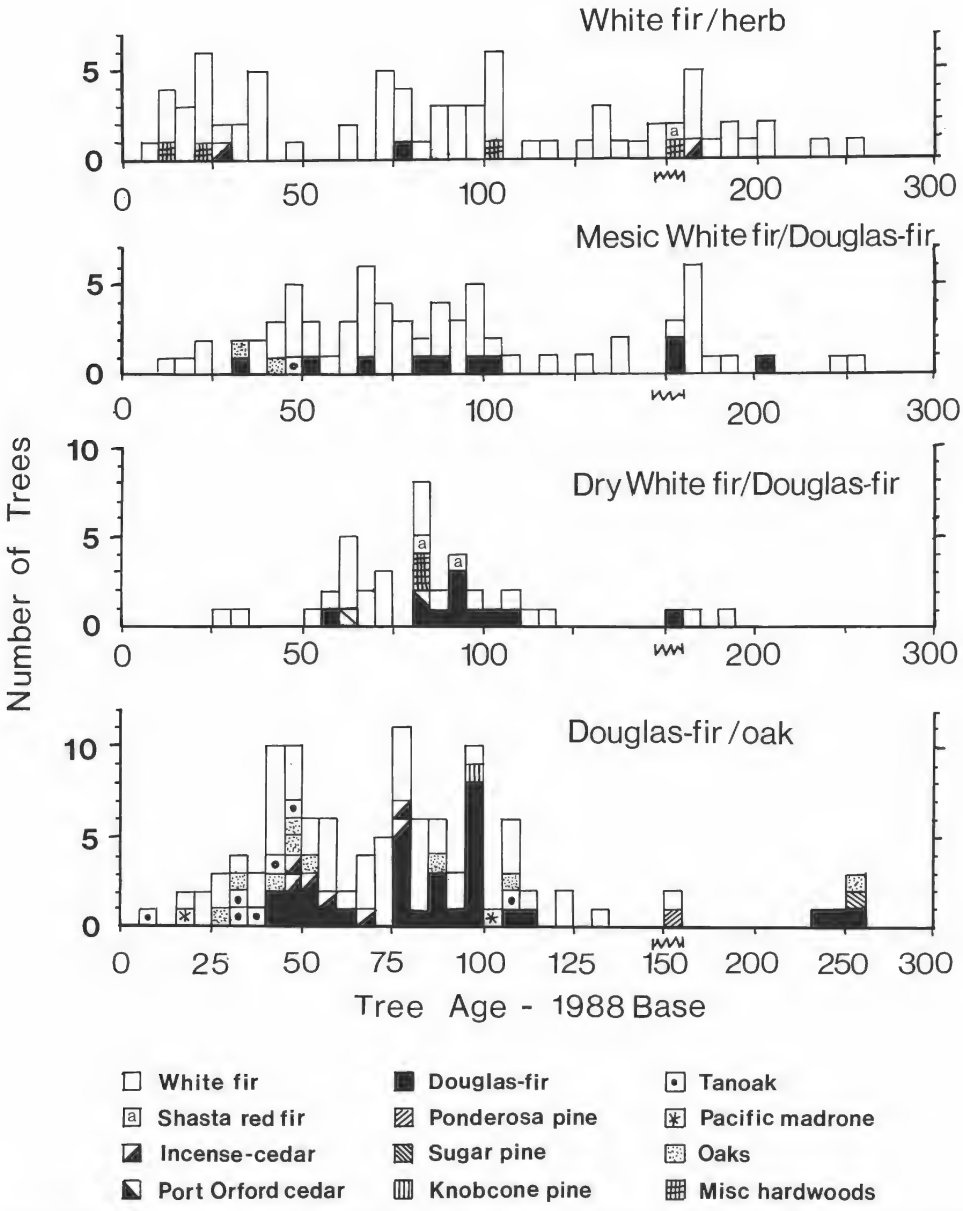

Figure 8. Age classes of forest tree species present in the major forest communities of Oregon Caves National Monument. Note that the horizontal scale changes from 5 years to 10 years at age 150 for each of the graphs. Species not previously identified in the text include: Shasta red fir (*Abies magnifica* var. *shastensis*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and tanoak (*Lithocarpus densiflora*).

nineteenth century had so increased fire frequency in the Siskiyou Mountains (Atzet and Wheeler 1982) that little trace was left of virgin stands in many areas. Yet the evidence for such claims, such as the area fire frequency of about 12 years between 1850 and 1920 across the extensive south-facing slope at Kinney Creek (Figure 5A), is not so different from the previous century (1760-1860) fire frequency of 16 years on the north-facing slope. This latter frequency estimate was made on a smaller area, which often increases the apparent fire return interval, and thus makes it a conservative estimate. Haefner's (1917) claims that southern Oregon did not experience forest fires prior to Euroamerican settlement are not justified.

The 1400-1989 natural fire rotation of 76 years for Oregon Caves (Table 2), although conservatively estimated, is similar to fire frequency in other dry Douglas-fir forests west of the Cascades. Natural fire rotations of 80 and 100 years have been estimated for dry Douglas-fir forests in western Washington (Agee and Dunwiddie 1984, Agee *et al.* 1990a), and for western Oregon (Morrison and Swanson 1990, Teensma 1987). If only the 1650-1930 period is considered, the overall NFR drops to 49 years, a more frequent fire history than most other Douglas-fir forests west of the Cascade Mountains (Agee, in press). The high fire frequency for Douglas-fir forest at Kinney Creek may be indicative of both a very dry, warm environment and the proximity of lower elevation types like ponderosa pine that, at least in other areas (e.g., McNeil and Zobel 1980), historically burned frequently. The close proximity of forest community types with typically different fire frequencies can result in a mixing of "typical" fire regimes (e.g., Agee *et al.* 1990a).

Old-growth Douglas-fir forests in southwest Oregon reflect the effects of multiple disturbances by fire. They will often be a mosaic of stands that contain very old trees and some younger age classes interspersed with other stands that were established after a stand replacement fire event. The landscape often has a patchy appearance created by interactions of fire frequency and severity, increasing forest structural and species diversity. Single fires separated by decades and those of low severity tend to result in Douglas-fir establishment, while ecosystems with fires closely spaced in time or severe fires have often favored knobcone pine, madrone, oak, or shrub species. Fire appears to have been a major determinant of historical landscape diversity in the Siskiyou Mountains. Future management scenarios, if they are to be successful, must recognize the inevitable flammability of this landscape, and the advantages of planning with fire as well as against it.

Acknowledgments

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1992 Annual Meeting of the Northwest Scientific Association

The Northwest Scientific Association will hold its 65th Annual Meeting on March 25-27 at Western Washington University, Bellingham, Washington. The meeting will be co-sponsored by the American Fisheries Society and the Society for Northwestern Vertebrate Biology. Symposium topics will include: "Biological Diversity and Its Implications" (March 25th) and "Assessment of Wetlands Function" (March 27th). In addition there will be an evening (March 25th) presentation by Tony Angell entitled "An Artistic Testimony to Understanding Nature." Contributed paper sessions and minisymposia will be developed in areas of Botany, Forestry, Geology, Marine Biology, and Zoology.

Northwestern Washington offers a rich diversity of ecosystems, and field trips will be scheduled to take advantage of this. Tentatively, these will include: survey of an old growth forest (Noisy Creek); Skagit River wetlands; lichens and early flowering plants (along the rocky shoreline); marine biology in the San Juan archipelago.

The deadline for abstract submission is January 24, 1992. Abstracts will be published in the May issue of *Northwest Science*. Students are encouraged to participate.

For additional information regarding the meeting, contact Dr. Ron Taylor, Program Coordinator, Biology Department, Western Washington University, Bellingham, WA 98225-9060.

Call for Applications to the Student Research Grants Awards Committee

A number of research grants *up to* $500 will be awarded to students. The successful recipients will be announced at the March meeting of the Northwest Scientific Association. Application forms can be obtained by writing to Dr. Ron Taylor, Chairman of the Awards Committee. Completed forms should be returned no later than 15 February 1992. The address to write for the form is:

Dr. Ron Taylor
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Call for Nominations

All members are encouraged to submit names for open positions in the Association and for honorary awards. Nominations for three Trustee positions should be mailed by 15 February 1992 to:

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and

William R. Gould, Montana Cooperative Fishery Research Unit, Biology Department, Montana State University, Bozeman, Montana 59717

Response of Underyearling Fluvial Arctic Grayling (*Thymallus arcticus*) to Velocity, Depth, and Overhead Cover in Artificial Enclosures

Abstract

Underyearling fluvial Arctic grayling (*Thymallus arcticus*) from Montana were tested in artificial enclosures to determine their responses to a range of water velocities and depths and overhead cover. Grayling occupied lower velocity water, shallower depths, and sites under cover in significantly greater proportions than were available. Knowledge of microhabitat feature preferences permits identification of likely rearing habitat and allows more effective sampling of age 0 fish and predictions of relative year class strength.

Introduction

The natural distribution of the Arctic grayling (*Thymalus arcticus*) in the western contiguous United States was limited to portions of the upper Missouri River drainage in Montana and Yellowstone National Park. Today the only known remaining native population of fluvial Arctic grayling is located in the Big Hole River in Montana. Because it is a declining population with a limited distribution, the fluvial grayling in Montana is designated as a "Species of Special Concern" by the Montana Department of Fish Wildlife and Parks and also by the Endangered Species Committee of the American Fisheries Society (Deacon *et al.* 1979).

Decline of this unique grayling population has stimulated several recent studies. Likness and Gould (1987) investigated the grayling's distribution, macrohabitat, and population characteristics. Sheppard and Oswald (1989) reported on grayling spawning runs and spawning sites. Kaya (1989) examined reotaxis of grayling fry and McMichael (1989) obtained information on the distribution and habitat of yearlings in the upper Big Hole River.

Field conditions can often make precise microhabitat preferences of fish difficult to define. This is true for the grayling inhabiting the stained waters of the Big Hole River where *in situ* observations are impractical. This study was undertaken to obtain information on use of water velocities, depths, and overhead cover by underyearling fluvial Montana grayling in artificial enclosures.

Methods

Test Enclosures and Underyearlings

Tests were conducted in enclosures in an indoor artificial stream located at the USFWS Bozeman Fish Cultural Development Center. The stream was an elongated doughnut shaped structure (Figure 1). Outside walls and bottom of the stream were constructed of plywood painted with black epoxy; the inside wall was glass to allow viewing.

The artificial stream was supplied with spring water circulated by a 5-speed electric trolling motor. The stream was lighted by overhead fluorescent lighting diffused through translucent white plastic sheets which supplied an average of about 14.9 microeinsteins/m^2/s (Wang 1989) at the water surface. The glass inner side of the stream was covered with black curtains having viewing ports.

Four similar test enclosures and a holding chamber were established in the artificial stream with screens (Figure 1). Each enclosure was 225 cm long by 61 cm wide by 40 cm deep and contained a riffle-pool-riffle sequence (Figure 2) constructed with 2-3 cm diameter gravel in depths from about 2-35 cm.

Grayling underyearlings tested were from embryos of Big Hole River adults raised at the Bozeman Fish Technology Center. Fish were placed in the holding chamber about 15 hours before being placed in the test enclosures to allow acclimation to temperature and confinement. Fish

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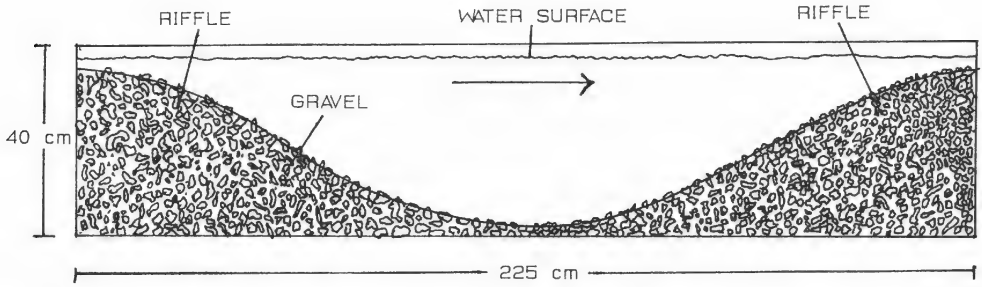

Figure 1. Diagram of artificial stream used in testing underyearling fluvial Montana Arctic grayling.

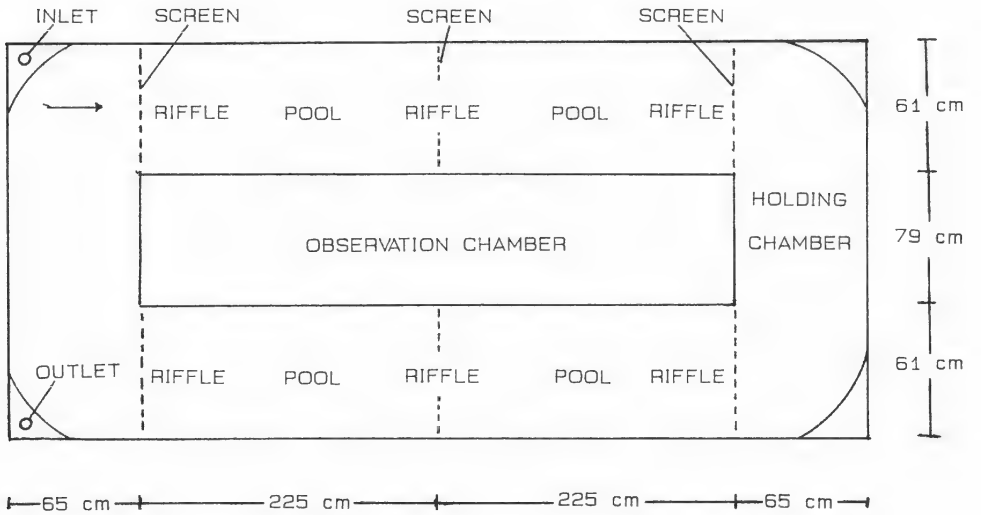

Figure 2. Diagram of enclosure used in tests of underyearling fluvial Montana Arctic grayling.

were fed while in the holding chamber, but not during tests.

Velocity and Depth Tests

Velocity and depth preference tests were conducted with 27 grayling 60-68 mm in total length from August 10-19, 1988. Fish were tested individually in enclosures 1, 2, and 4 (Figure 1). Beginning 15 minutes after introduction into the test enclosure, the velocity and depth of each fish was measured at 15 minute intervals for 2.0-2.5 hours. Velocity and depth measurements were made with a Montedoro-Whitney model PVM-2A current meter and recorded to the nearest 0.1 cm/s and 0.5 cm depth. Taking measurements disturbed fish for no longer than 30 s.

The velocities and depths available to fish (Table 1) in enclosures 1, 2, and 4 were determined by mapping the enclosures after all of the tests had been completed. Strings were taped across the top of each test enclosure to create a grid of 10 x 10 cm squares. The velocity was measured in 10 cm increments starting at a 5 cm depth. Velocity was measured in the center of each 1000 cm^3 cell. If the remaining depth was less than 10 cm, a final velocity was recorded at one-half the remaining distance. The maximum depth of each cell was recorded as the available depth. The test results from enclosure 3 were not reported because the bottom gravel was inadvertently disturbed prior to measuring enclosure velocities. Temperatures were 16.5-18.0°C during tests.

TABLE 1. Percentages of depth and velocity classes present within the enclosures used for testing underyearling fluvial Arctic grayling.

Parameter	Enclosure number		
Depth (cm)	1	2	4
1-9	4.28	9.33	6.63
10-19	18.64	15.03	14.93
20-29	35.54	32.36	47.23
≥30	41.52	43.26	31.20
Velocity (m/s)			
0.00-0.09	76.89	71.50	85.60
0.10-0.19	19.52	28.33	14.42
0.20-0.29	3.30	0.18	0.00
≥0.30	0.27	0.00	0.00
Total volume (cm^3)	329,200	275,100	292,000

Overhead Cover Tests

From August 26-30, 1988, 48 grayling 70-80 mm in total length were used in cover preference tests. Fish were tested individually in all four enclosures (Figure 1); one-half of the length of each enclosure was covered by a sheet of plywood and the other half was uncovered. In successive trials the position of the overhead cover was moved from over one side of the enclosure to the other to equalize the effect of the slight habitat differences between sides. The position of each fish in relation to the overhead cover was observed at 10 minute intervals for 1.5 hours beginning no sooner than 5 minutes after the fish were introduced into the enclosure. Water temperatures were 14.8-16.4°C during tests.

Statistical Analyses

The respective velocities and depths within each enclosure were grouped into four classes. Each class was constructed to contain about 25 percent of the total volume in its enclosure. The available volumes of these velocities and depth classes were then compared to actual grayling use of these classes by one way chi-square analyses (Lund 1987). Use of cover by grayling was tested with a binomial probability test (Lund 1987).

Results

The use of velocity classes by Arctic grayling (Table 2) was not proportional to their availabilities in any of the three test enclosures ($P < 0.01$ for each enclosure). Fish used the lower velocity classes (≤4 cm/s) in all enclosures in greater proportions than the volumes of these classes provided.

Grayling use of depth classes (Table 3) also was disproportional to their available volumes in all enclosures ($P < 0.01$ for each enclosure). Underyearlings made proportionally greater use of the upper 21 cm of the enclosures and less use of depth classes below 30 cm. Furthermore, grayling used areas with overhead cover significantly more often ($P < 0.01$) than areas without cover (Table 4).

TABLE 2. Proportions of velocity groups present in test enclosures and use of velocity groups by underyearling fluvial Arctic grayling.

Variable				
	Enclosure 1			
Velocity group (cm/s)	0-4	5-6	7-10	11-31
% tank volume	29.2	26.8	24.2	19.8
Number (%) grayling locations	41(46)	25(28)	17(19)	7(8
	Enclosure 2			
Velocity group (cm/s)	0-3	4-6	7-9	10-20
% tank volume	21.2	26.5	23.8	28.5
Number (%) grayling locations	33(37)	25(28)	13(15)	18(20
	Enclosure 4			
Velocity group (cm/s)	0-2	3-4	5-7	8-17
% tank volume	19.6	23.0	29.6	27.8
Number % grayling locations	36(43)	21(25)	13(15)	14(17

TABLE 3. Proportions of depth groups present in test enclosures and use of depth groups by underyearling fluvial Arctic grayling.

Variable				
	Enclosure 1			
Depth group (cm)	0-21	22-27	28-31	32-34
% tank volume	25.4	21.9	28.7	24.0
Number (%) grayling locations	45(50)	22(24)	22(24)	1(1
	Enclosure 2			
Depth group (cm)	0-19	20-27	28-31	32-34
% tank volume	24.4	29.3	25.0	21.3
Number (%) grayling locations	47(52)	23(25)	15(17)	5(6
	Enclosure 4			
Depth group (cm)	0-20	21-26	27-29	30-33
% tank volume	25.0	22.9	20.9	31.2
Number % grayling locations	38(42)	25(28)	25(28)	2(2

TABLE 4. Use of cover by underyearling fluvial Arctic grayling from Montana in 1988. Specimens were 70-80 mm in total length.

Enclosure	Number of fish	Number of observations	
		Under cover	Not under cover
1	12	91	29
2	12	90	30
3	12	86	34
4	12	103	17
Totals	48	370	110

Discussion

Microhabitat preferences of fish can often be more precisely defined in the laboratory than in the field. This is certainly true for the grayling living in the stained waters of the Big Hole River where *in situ* observations are impractical. About 85 percent of the underyearling grayling were in waters of 0-10 cm/s. This range of velocities is less, and more closely identifies preferred velocities than the reports of juvenile grayling using areas with mean water column velocities of 0.18-0.24 m/s (Elliot 1980, Kreuger 1981, Hubert *et al.*, McMichael 1989).

In 97 percent of our observations, grayling underyearlings were found to be in water depths of 31 cm or less. This distribution is virtually the same as the depth estimated by the suitability index curve developed by Hubert *et al.* (1985) from field data.

Young grayling are often associated with some type of cover. In this study, they also used overhead cover. In Alaska, young grayling used interstitial spaces and the shadows of boulders as cover (Kreuger 1981), and in the Big Hole River young-of-the-year grayling were often captured within 30 cm of aquatic plants, suggesting vegetation served as cover (McMichael 1989).

The well-being of fluvial grayling (and other populations) is directly dependent on underyearling survival. Evaluations of underyearling abundance can allow managers to assess potential year class strengths more readily and easily than most other methods. Knowledge of the preferred microhabitat permits managers to identify and effectively sample age 0 fish habitat and better predict year class strengths.

Acknowledgments

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Spruce Beetle Attacks and Surviving Beetle Brood in Limbed and Bucked Spruce in South-Central Alaska

Abstract

The current policy in south-central Alaska for treatment of spruce slash to prevent increase of spruce beetle populations is to limb felled trees that remain on the site and buck the stems into bolts about 0.6 m long. In this study, bucking of stems into short lengths, a costly treatment which failed to reduce bark moisture content, also failed to reduce beetle attack densities or numbers of brood that developed into adults. Limbed bolts, however, produced fewer two-year adults than unlimbed bolts on warm sites, but not on cool sites where numbers of two-year adults were low in both limbed and unlimbed bolts. This information should assist land managers in developing flexible policies for treatment of spruce slash.

Introduction

Right-of-way clearings for highway and powerline construction result in large quantities of spruce (*Picea* spp.) slash and debris. If left untreated, spruce slash can contribute substantially to build-up of spruce beetle (*Dendroctonus rufipennis* Kby.) populations (Schmid 1977) because downed spruce, whether windfelled or cut, are preferred by spruce beetles over standing live spruce (Schmid and Beckwith 1975, Schmid 1981). When downed spruce are not burned or removed, the current policy in south-central Alaska is to limb spruce slash and buck stems that are 15 cm or larger in diameter to about 0.6-m lengths. The rationale for the more labor intensive procedure of bucking is that short bolts should dry more rapidly than long bolts and should thus reduce survival of spruce beetle brood. Therefore, the number of surviving brood that could spread from slash to surrounding live trees should be reduced.

Bucking of slash into short lengths has proven effective for restricting spruce beetle numbers in areas with warm, dry summers such as in the southern Rocky Mountains (Mitchell and Schmid 1973). The primary objective of this study was to determine whether bucking of felled spruce on the Kenai Peninsula into 0.6-m bolt lengths would effectively reduce numbers of spruce beetle attacks and new adults as compared to bolts 2 times, 4 times, or 8 times longer. Secondary objectives were to determine the effects of sample location along bolt surfaces and the effects of limbing on those same response variables.

Study Areas and Methods

The experiment was conducted at five areas on the Kenai Peninsula: three sites near mileposts (MP) 14, 34, and 64 on the Seward Highway north of Seward, a site at Tern Lake near the junction of the Seward and Sterling Highways, and a site at the south end of Snug Harbor Road on Kenai Lake near Cooper Landing. Differences in summer climate and spruce species among study areas suggested a randomized block experimental design with the five study areas as experimental blocks. Sites at MP14 and MP34 lie within a cold-wet fire season climatic zone based on integration of precipitation effectiveness index and temperature efficiency index whereas the remaining study sites lie within a warm-dry fire season climatic zone (Trigg 1971).

In April 1987, eight mature Sitka spruce (*P. sitchensis* (Bong.) Carr.) at MP 14, and eight mature Lutz spruce (*P.* x *lutzii* Little), the hybrid of Sitka and white spruce (*P. glauca* (Moench) Voss), at each of the four remaining sites were felled into openings exposed to the sun. All sample trees were roughly equal in diameter at 1.7-m height.

Four trees selected at random were limbed and the remaining four trees were left unlimbed at each study area. The lower 9.2-m bole length of each tree in each study area was bucked into four bolts of differing lengths. To ensure that each of the four selected lengths was distributed among the larger and smaller bole diameters, each limbed and unlimbed tree in each experimental block were

randomly assigned without replacement one of the following bucking sequences from lower to upper bole:

A. 0.6 m, 1.2 m, 2.4 m, 4.9 m
B. 1.2 m, 2.4 m, 4.9 m, 0.6 m
C. 2.4 m, 4.9 m, 0.6 m, 1.2 m
D. 4.9 m, 0.6 m, 1.2 m, 2.4 m

Therefore, the four sequences were replicated twice in each block. Cut ends of adjacent bolts were separated for increased exposure to the air and sun to hasten drying, and bolts were left in place for subsequent spruce beetle attacks.

Four 2-cm diameter bark disks were removed in late June from each bolt at mid-length; one from the bottom side, one from each lateral side, and one from the top side. Disks from each bolt were combined and frozen in a separate small plastic bag for laboratory determination of bark percent moisture content on a dry-weight basis. Bark was re-sampled in the same manner in August to determine degree of drying by the end of the first summer.

Four of the experimental trees in each study area were randomly selected for spruce beetle sampling in the early fall of 1987. Four 15.24-cm by 15.24-cm bark squares were removed from each tree bolt at mid-length, one from the upper surface, one from the lower surface, and one from each side to determine mean numbers of attacks and recently matured adults visible at the cambial surface. In south-central Alaska, a variable proportion of beetles, depending on exposure to warm temperatures, matures by the end of the first summer and the remainder matures during the second summer (Werner and Holsten 1985). These beetles are referred to, respectively, as "one-year" and "two-year" adults.

The remaining sample trees were sampled in the early fall of 1988 to determine densities of two-year adults, but twelve 45.6 cm^2 bark disks (diameter = 7.6 cm) were removed from each bolt, four about 15 cm from each end and four from midbolt. Each subset of four disks was distributed around the circumference of the bolt as with 1987 samples.

Larger numbers of samples were taken per bolt in 1988 to assess the effect of horizontal as well as vertical positioning along the bolt on production of two-year adults. Smaller individual samples were chosen in 1988 because they were considered adequate to assess two-year adult populations, which are usually higher than densities of attacks of one-year adults, and because the smaller samples could be dissected more easily. Dissection allowed accurate counts of two-year adults that were distributed throughout the phloem in each sample disk.

Numbers of beetle attacks and one-year or two-year adults per 100 cm^2 were transformed to natural logarithms, Ln (X + 1). These data were analyzed by the General Linear Models (GLM) multivariate analysis of variance (MANOVA), a procedure appropriate for balanced data (SAS Institute 1987), to test for (a) significant differences in spruce beetle attacks and (b) new adults among sample areas, sample bolt lengths, and position on sample bolts.

By mistake, only one limbed tree versus three unlimbed trees at MP 14 and three limbed trees versus one unlimbed tree at Snug Harbor were chosen for sampling in 1987. This left three limbed trees versus one unlimbed and one limbed versus three unlimbed trees at MP 14 and Snug Harbor, respectively, for sampling in 1988. Only limbed trees were sampled in 1987 and only unlimbed trees were sampled in 1988 at MP 64. Therefore effect of limbing on density of two-year adults, only, was analyzed by the GLM procedure for unbalanced data analysis of variance (ANOVA) (SAS Institute 1987), but MP 64 data were excluded. Densities of attacks and one-year adults were eliminated from this analysis because there were no apparent differences in means between limbed and unlimbed bolts (Fig. 2AB).

Because separate variables measured on the same sample units are commonly correlated, significance level for all analyses was set conservatively at *Alpha* = 0.01.

Results and Discussion

Sample block was significant for densities of attacks and two-year adults (Table 1A), so blocking by study area in a randomized block experimental design was effective (Lentner *et al.* 1989).

Bolt length had no significant effect on any response variable (Table 1A, Table 2). Mean bark moisture content generally differed little between June and August 1987 among limbed or unlimbed bolts regardless of bolt length for combined experimental blocks from warm-dry or cold-wet zones (Figure 1AB). We do not know why bark moisture remained high through the summer but the Kenai

TABLE 1. Probability of a greater F for spruce beetle response variables by sources of variation. A. GLM MANOVA for all study areas and B. GLM ANOVAs for all study areas except Granite Creek.

Source of Variation	1987 Attacks	1987 One-year adults	1988 Two-year adults
A.			
Sample block	0.0001	0.012	0.006
Bolt length	0.74	0.65	0.76
Bolt position[a]			0.02
Bolt side	0.0001	0.0001	0.0001
Interactions:[b]			
Position x side			0.006
B.			
Limbing			0.33

[a]Butt end, middle, or upper end of bolts sampled in 1988
[b]Only those that were significant.

Peninsula is not arid (U.S. Department of Commerce 1989). Furthermore, sample trees in most areas were moistened several times by light rains and by dew from adjacent tall grasses (*Calamagrostis* spp.), that occupy many natural clearings.

Bolt side had a significant effect on mean densities of attacks and densities of one- and two-year adults (Table 1A), with highest mean densities usually occurring on the bottom side and lowest numbers on the top side. This pattern follows the distribution reported for spruce beetles in logging slash in British Columbia (Dyer and Taylor 1971) and windfelled spruce in the Rocky Mountains (Schmid 1981), which was attributed to the beetle's preference for attacking shaded host material and to higher brood mortality in upper bole surfaces during both winter and summer.

Mean densities of two-year adults were consistently higher at mid-bolt than at the bolt ends regardless of bolt length (Table 3). Whether the slightly lower mean densities of adults near bolt ends were a result of more rapid phloem deterioration, higher brood parasitization, or predation is unknown because parasite and predator populations were not monitored.

The interaction of bolt position x bolt side was significant for two-year adults (Table 1A) presumably because approximately equal mean densities on bottom and lateral sides occurred at the upper ends, only, of bolts (Table 3). This resulted in non-parallel curves of two-year adult

TABLE 2. A. Spruce beetle attacks, B. one-year adults, and C. two-year adults per 100 cm^2 (X ± SE).

Bolt Length (m)		Study Area MP 14	MP 34	Tern Lake	Snug Harbor	HP 64
A.						
0.6		0.38 ± 0.11	0.66 ± 0.10	0.68 ± 0.16	0.70 ± 0.14	0.45 ± 0.09
1.2		0.25 ± 0.08	1.15 ± 0.16	0.39 ± 0.10	0.95 ± 0.20	0.38 ± 0.14
2.4		0.09 ± 0.05	0.91 ± 0.16	0.48 ± 0.12	0.83 ± 0.19	0.34 ± 0.11
4.9		0.23 ± 0.10	0.81 ± 0.14	0.77 ± 0.13	0.63 ± 0.14	0.39 ± 0.11
	Mean	0.24 ± 0.04	0.88 ± 0.07	0.58 ± 0.07	0.78 ± 0.08	0.39 ± 0.05
B.						
0.6		0.20 ± 0.07	0.54 ± 0.22	1.06 ± 0.38	1.04 ± 0.31	0.41 ± 0.16
1.2		0.25 ± 0.07	1.09 ± 0.49	0.45 ± 0.13	0.34 ± 0.19	0.26 ± 0.14
2.4		0.27 ± 0.18	0.66 ± 0.24	1.31 ± 0.67	0.65 ± 0.26	0.43 ± 0.20
4.9		0.36 ± 0.16	0.61 ± 0.23	0.72 ± 0.27	1.11 ± 0.33	0.48 ± 0.22
	Mean	0.27 ± 0.06	0.73 ± 0.16	0.88 ± 0.20	0.78 ± 0.14	0.41 ± 0.09
C.						
0.6		3.44 ± 0.93	3.32 ± 0.86	3.11 ± 0.73	3.62 ± 0.96	4.92 ± 1.24
1.2		1.71 ± 0.46	3.26 ± 0.85	3.20 ± 0.54	6.09 ± 1.04	6.70 ± 1.31
2.4		1.92 ± 0.47	1.77± 0.47	4.90 ± 1.17	9.17 ± 1.54	8.13 ± 1.86
4.9		3.44 ± 0.80	1.22 ± 0.40	3.93 ± 1.15	6.27 ± 1.05	4.71 ± 1.36
	Mean	2.63 ± 0.35	2.38 ± 0.34	3.78 ± 0.47	6.29 ± 0.60	6.24 ± 0.75

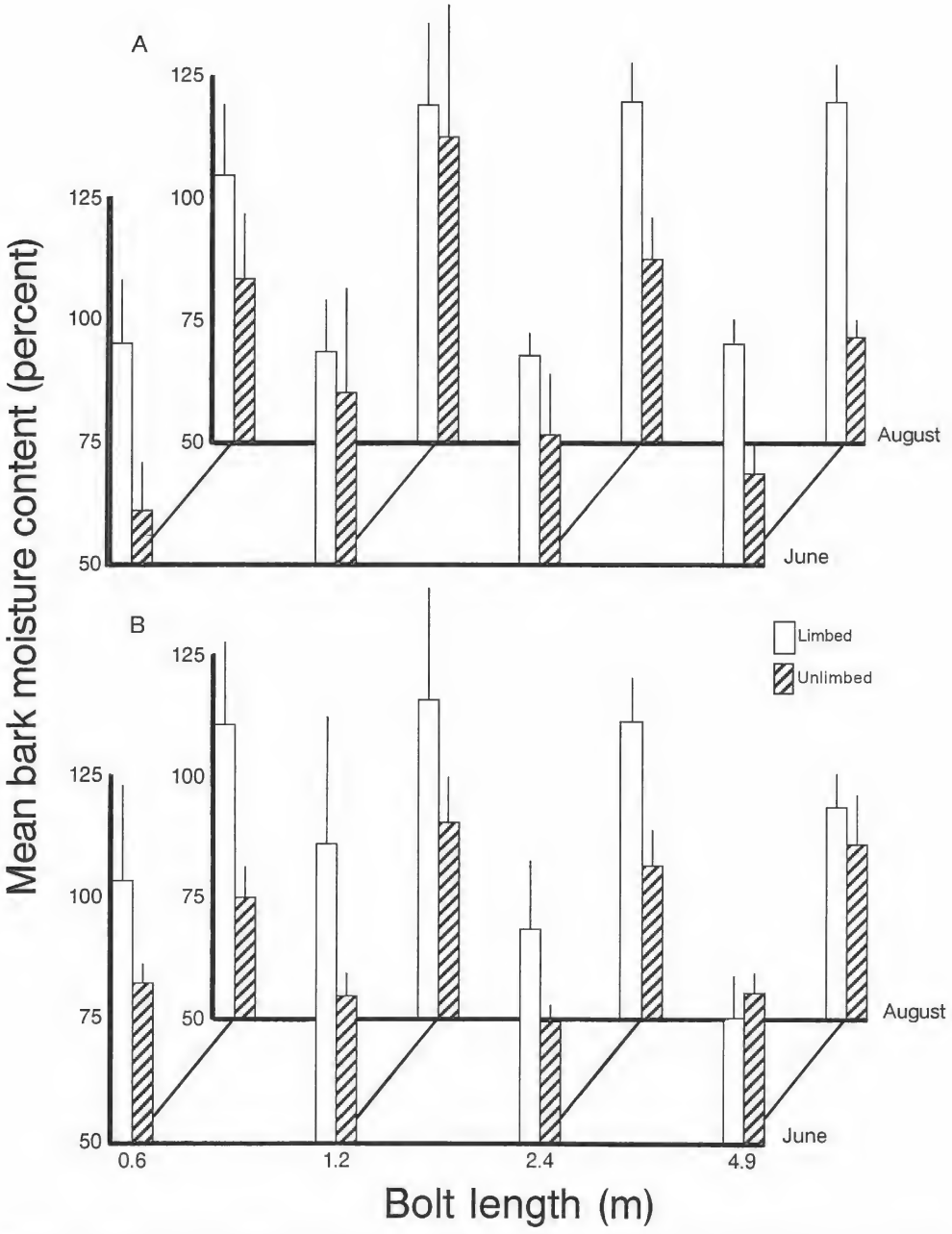

Figure 1. Mean bark moisture content by bolt length and 1987 sample month, A. Warm-dry zone (Trigg 1971): Tern Lake and Snug Harbor combined B. Cold-wet zone (Trigg 1971): MP 14 and MP 34 combined. Vertical lines extending above bars equal one SE.

TABLE 3. Spruce beetle two-year adults per 100 cm² in limbed versus unlimbed bolts from all study areas (X ± SE).

Sample			Bolt Length (m)			
Position	Side	Limbed	0.6	1.2	2.4	4.9
Butt	Bottom	Yes	6.30 ± 2.94	3.45 ± 1.50	6.30 ± 2.05	2.74 ± 1.48
		No	7.31 ± 3.36	4.20 ± 1.47	7.68 ± 2.10	5.18 ± 1.63
	Lateral	Yes	0.69 ± 0.29	1.64 ± 0.78	2.19 ± 1.04	1.92 ± 1.05
		No	3.02 ± 1.19	4.39 ± 0.89	5.03 ± 1.54	2.29 ± 0.92
	Top	Yes	0.55 ± 0.55	2.19 ± 1.61	0.55 ± 0.55	0.27 ± 0.27
		No	2.74 ± 1.33	3.47 ± 1.54	5.67 ± 2.01	2.79 ± 1.42
	Mean		3.58 ± 0.89	3.38 ± 0.55	4.88 ± 0.76	2.67 ± 0.54
Middle	Bottom	Yes	3.56 ± 2.75	7.95 ± 3.24	3.56 ± 1.09	4.11 ± 2.67
		No	6.98 ± 1.41	8.04 ± 3.08	12.43 ± 3.60	11.16 ± 3.20
	Lateral	Yes	0.82 ± 0.45	1.37 ± 0.78	2.47 ± 1.01	2.47 ± 1.12
		No	4.57 ± 1.18	6.67 ± 2.09	5.12 ± 1.42	6.28 ± 2.10
	Top	Yes	2.19 ± 1.24	0.82 ± 0.58	1.10 ± 0.83	0.00
		No	3.59 ± 1.71	5.67 ± 1.78	4.57 ± 1.99	3.79 ± 1.75
	Mean		3.86 ± 9.66	5.43 ± 0.97	5.37 ± 1.00	5.06 ± 0.99
Upper	Bottom	Yes	3.56 ± 1.60	3.84 ± 0.99	1.92 ± 1.34	1.64 ± 0.90
		No	6.18 ± 1.91	4.75 ± 1.47	7.68 ± 4.01	6.78 ± 2.57
	Lateral	Yes	0.41 ± 0.29	3.15 ± 1.14	1.37 ± 0.58	4.66 ± 1.01
		No	4.75 ± 0.86	7.04 ± 1.72	8.50 ± 2.67	6.18 ± 1.74
	Top	Yes	4.93 ± 2.51	1.37 ± 0.82	0.55 ± 0.55	0.00
		No	1.10 ± 0.57	1.46 ± 0.78	7.68 ± 3.81	2.59 ± 1.14
	Mean		3.55 ± 0.62	3.76 ± 0.58	5.28 ± 1.28	3.89 ± 0.72

densities plotted by bolt sample side over bolt longitudinal position, and thus an interaction effect.

The pervasively higher numbers of two-year adults from unlimbed samples (Table 3) results partially from inclusion of samples from MP 64 which were taken only from unlimbed trees. Results of ANOVAs that excluded MP 64 data showed, however, that limbing had no consistent effect on two-year adult beetle density (Table 1B). Higher densities of two-year adults were found in unpruned bolts only at Tern Lake and Snug Harbor (Figure 2A) near Cooper Landing which has warm, dry summers, whereas MP34 and MP14 are closer to Seward and its maritime climate where cooler, wetter summers prevail.

Mean percent bark moisture content was usually lower in unlimbed bolts (Figure 1AB), apparently because moisture continued to transpire through intact foliage (Johnson and Zingg 1969). These results suggest that limbing may affect production of two-year adults by inhibiting changes in bark moisture content and through increases in daytime bark temperature.

Optimum phloem temperatures for spruce beetle oviposition (Sahota and Thomson 1979), brood development (Dyer *et al.* 1968), or survival (Dyer and Taylor 1971) may be exceeded on limbed trees in warm-dry zones. Conversely, limbing in cold-wet zones may allow phloem temperatures to rise to near optimum levels. Hard (in press) showed that in standing spruce on a warm site, pruned boles were successfully attacked less often by spruce beetles than were unpruned boles. Furthermore, trees with subcortical bark temperatures that exceeded 18°C at solar noon during beetle mass-attacks had fewer successful attacks than trees with lower bark temperatures.

Conclusions

Bucking of downed spruce into short lengths did not hasten drying of bark or reduce emerging spruce beetle populations on the Kenai Peninsula, but limbed bolts had lower densities of two-year adults in warm-dry areas. These results should not be extrapolated, however, to areas off the Kenai Peninsula.

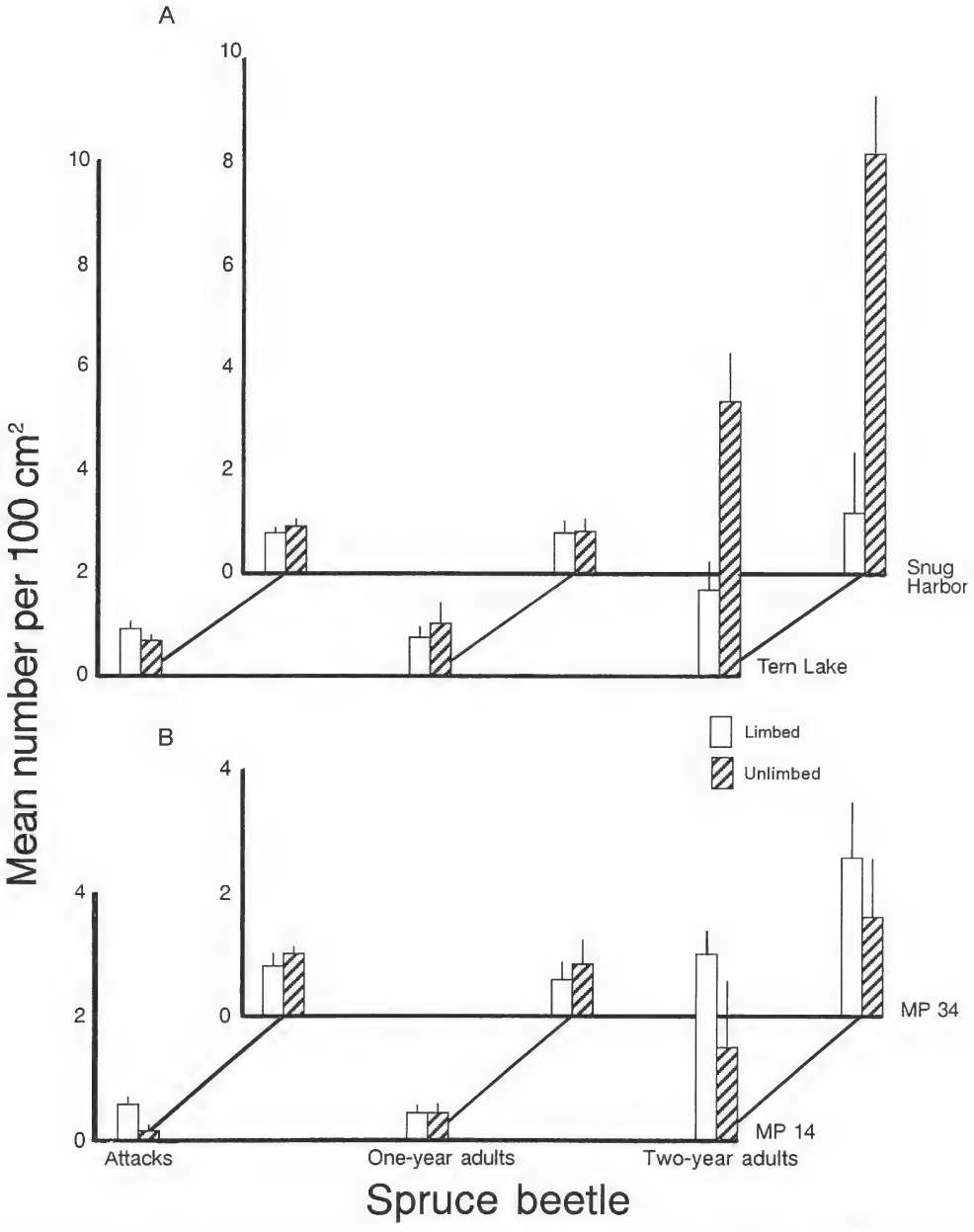

Figure 2. Mean numbers of attacks, one-year adults, and two-year adults from limbed and unlimbed bolts, A. Warm-dry: Tern Lake and Snug Harbor, B. Cold-wet: MP 14 and MP 34. Vertical lines extending above bars equal one SE.

Where spruce slash cannot be burned, treated with pesticide, or removed to prevent beetle population increase, scattering limbed and bucked stems in lengths necessary only to facilitate handling in cleared areas most exposed to the sun may be practical. Limbing and scattering may not prevent beetle population increase in spruce slash but it should slow the rate of increase in areas with warm-dry summers where spruce beetle outbreaks are typically more intense.

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Mountain Goat Population Trends in the Olympic Mountain Range, Washington

Abstract

We conducted an extensive aerial census of introduced mountain goats (*Oreamnos americanus*) in the Olympic Mountains during July 1990 to track population trend. The population in the 50,063 ha census zone was estimated with a stratified random block design at 389 ± 106 (SE) goats, significantly lower than an estimate in 1983. The large SE occurred despite improved information on goat densities being used to stratify the census blocks, and could reflect greater relative clumping of goats at lower population levels. The smaller 1990 population probably resulted from removals by the National Park Service combined with more severe winters.

Introduction

Mountain goats have colonized virtually the entire Olympic Mountain Range since their introduction in the 1920's (Moorhead and Stevens 1982). Olympic National Park was established as a natural area in 1938; goats are viewed now as an undesirable, introduced species by the National Park Service (NPS, Environmental assessment on mountain goat management in Olympic National Park 1981, 1987). In 1981, the NPS launched a program to remove goats from the park, which continued with varying intensity through 1989 (Houston *et al.* 1991). Determining goat population levels and trends is important to park managers. An initial helicopter census conducted in July 1983 returned an estimate of 1175 ± 171 (SE) goats (Houston *et al.* 1986). Here we report the results from a second range-wide census conducted during July 1990.

Study Area and Methods

The rationale for choosing the particular helicopter census design has been previously described (Houston *et al.* 1986). Briefly, most goats are seasonally migratory and visible mainly during midsummer on subalpine ranges above 1500 m. The census zone included all of the 50,063 ha of land free of glacial ice above 1520 m (5000 feet) in the Olympic Mountains. About 87% of the area is now within the park; a slight increase (ca. 2%) over 1983 resulted from 1986 boundary changes with Olympic National Forest (readers need to be aware of these changes if maps of the 1983 and 1990 counts are compared). A block count sampling method was used and four census strata were recognized:

(1) Known or suspected high density goat areas: Olympus, Chimney, Flapjack, Royal, Constance, Buckhorn (Figure 1). 6229 ha total area. Aerial total counts were conducted in each of these units.

(2) Known or suspected medium density goat areas. 12,267 ha. These were divided into 24 blocks of about 500 ha each. Sixteen blocks (66%) were chosen randomly and censused.

(3) Known or supsected low density goat areas (densities thought to be 0.20 goats/km^2 or less). 29,570 ha. These were divided into 59 blocks of about 500 ha each. Fifteen blocks (25%) were chosen randomly and censused.

(4) Klahhane Ridge. 1997 ha. An aerial total count was conducted. This stratum was retained because it has been the focus of intensive population (Houston and Stevens 1988) and vegetation studies (Pfitsch and Bliss 1985, E. G. Schreiner pers. comm.) and a total count was considered necessary, although goat numbers were now thought to be very low.

The population estimate for strata 2 and 3 was calculated with Jolly's (1969) method for unequal-sized sample units, as outlined by Norton-Griffiths (1976:72). This approach uses the density of goats rather than the number observed per block to produce estimates, which was necessary due to the variation in block sizes ($\bar{X}$ = 504 ± 52.9 SD ha). As in 1983, the counts for strata 1 and 4 were added, without variances, to the estimates for strata 2 and 3, a move analogous to "stratifying out large herds" (Norton-Griffiths 1978:84).

Several steps were taken to maintain comparability between counts and to attempt to improve the precision (repeatability) of the 1990 count:

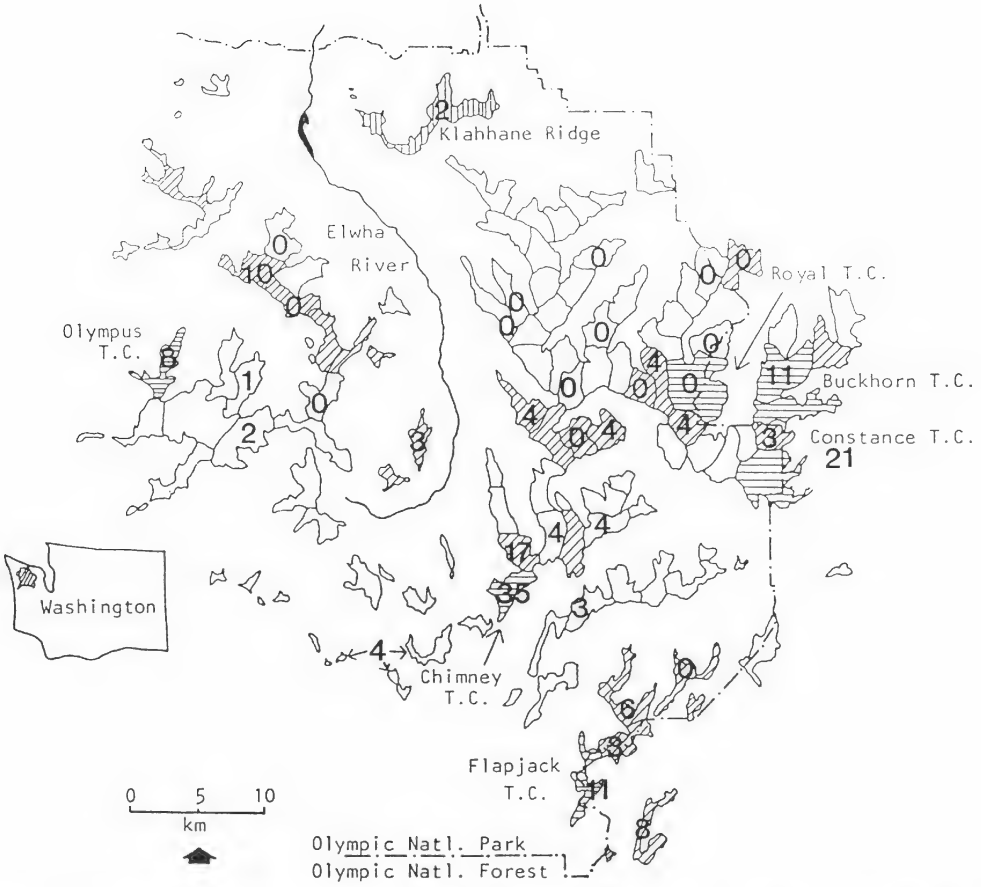

Figure 1. Number of mountain goats counted per census unit, Olympic Mountains, July 1990. Total count (T.C.; horizontal hatch), Klahhane Ridge, medium density (diagonal hatch) and low density (open) areas are indicated. Extensive areas of glacial ice are not shown.

(1) Census procedures were similar. Lower boundaries of each unit were flown first, and the unit was then searched upslope at 70-100 m intervals at speeds of 40-70 mph. A maximum of 30 minutes was allocated for counting each block; actual counting time averaged 18.8 ± 7.15 minutes (0.044 ± .036 min/ha; which compares to about 0.038 min/ha in 1983). No time limit was placed upon counting the units in strata 1 and 4, but search effort was similar to the blocks (.041 ± .015 min/ha).

(2) The three person census team was composed, for the most part, of the same individuals in both counts. However, during 1990 a Hughes 500-D helicopter was used instead of the Aerospatiale A-Star 350D of 1983.

(3) Generally, the boundaries of the counting units were the same in both censuses. However, by 1990, more information on relative goat densities was available throughout the park following extensive aerial capture efforts conducted from 1985 to 1989 (ca. 50-60 flight hours/year). Presumptive goat densities in all park units, therefore, were reevaluated and, where necessary, units were restratified by density class. Information on goat harvest trends and hunter observations of goats (Washington Dept. Wildlife, Unpubl.) was used to restratify units outside the park.

4) Wide variation in goat densities counted during 1983 within putative medium density areas contributed substantially to a standard error that was about 15 percent of the population estimate (Houston *et al.* 1986). In addition to restratifying the counting units in 1990, we increased both the intensity of sampling for medium density blocks (66% in 1990 vs. 47% in 1983) and the number of high density total count units (6 vs. 3) to attempt to reduce the SE.

Bias errors. Aerial census is known generally to underestimate the actual numbers of animals present (e.g., Caughley 1977, Norton-Griffiths 1978), and this is true for mountain goats as well (Houston *et al.* 1986). Three estimates of the bias error for goats in the census zone were available: (1) Johnson (1983:68) used ratios of marked to unmarked goats observed during a 1981 helicopter count to calculate a bias error of .37 (i.e., a "sightability" or census efficiency of .63) in the Charlia Lakes area of the northeast Olympics. (2) Houston *et al.* (1986) estimated a mean bias of .34 ± .05 (.66 sightability) from 3 "index-manipulation-index" estimates (Caughley 1977:47) for Klahhane Ridge using the extensive goat removals of 1981-1983. (3) Hoffman (1987) estimated a bias of .29 ± .17 (.71 sightability) using up to 7 radio-collared goats/count during 5 censuses of the Mt. Appleton and Mt. Carrie areas during 1985-1986.

Sightability probably varies among counting units in the census zone (Houston *et al.* 1986) and within the same unit over time; however, the available estimates of bias error are broadly similar. Consequently, we used the estimate of 0.66 sightability (also used in 1983) to produce a more accurate estimate (i.e., nearer the true total) for the 1990 count. The number of goats observed in each census unit was therefore multiplied by 1.52 (the reciprocal of 0.66). Clearly, use of the bias error constant only expands the estimates uniformly; it does not otherwise enhance aspects of statistical rigor.

Results and Discussion

The census was conducted in seven early morning flights between 16-31 July. Total census time (including travel among counting blocks and refueling stations) was 21.3 hours.

A total of 172 goats (136 adults, 36 kids) was counted in the 4 strata (Fig. 1, Table 1). Counts were highly variable within the medium density stratum and total count units.

The estimated goat population for strata 2-3 ($\hat{Y}_{2-3}$) was calculated as:

Stratum	$\hat{Y}_h$	$\mathrm{Var}(\hat{Y}_h)$
2 (low density)	104.3	1,095.1
3 (medium density)	150.5	10,157.8
Total	255	11,252.9

The standard error ($\hat{Y}_{2-3}$) is $\sqrt{\mathrm{Var}(\hat{Y}_{2-3})}$ or 106 goats. When the 131 goats in the high density units and the 3 from Klahhane Ridge are added, $\hat{Y}_{1-4}$ totals 389 ± 106 (SE) goats for the population in the census zone during July 1990.

We were unsuccessful in reducing the relative SE (27% of the estimated population) by restratifying the blocks and re-allocating the sampling effort. This may reflect greater relative clumping of goats at lower population levels. It *may* be possible to reduce the SE in future counts by modifying the census design. This could include conducting restratification flights immediately prior to the census and attempting to optimize sampling effort during the count (Gasaway *et al.* 1986).

Despite the large standard errors, the 1990 population estimate differed significantly from the 1983 estimate of 1175 animals (t test $\propto_{0.05[2]}$, $t_{calculated} = 3.90$, Norton-Griffiths 1978:80, Gasaway *et al.* 1986:62) and we conclude that goat numbers declined considerably over the seven

TABLE 1. Area sampled and mountain goats counted in the Olympic Range, July 1990.

Stratum	Area (ha)	No. Blocks	Area Sampled	Blocks Sampled	Goats Counted	Adjusted Goat Numbers[1]
1) High Density	6,229	--	6,229	--	86	130.7
2) Low Density	29,570	59	7,686	15	18	27.1
3) Medium Density	12,267	24	8,158	16	66	100.1
4) Klahhane	1,997	--	1,997	--	2	3.0

[1]Numbers observed x 1.52 for all strata.

years. Striking differences occurred between counts in five of seven large areas censused both years (Table 2). There were no differences, however, in group sizes ($n = 162\ \bar{X} = 2.74 \pm 3.51$ goats in 1983; $n = 84\ \bar{X}\ 2.05 \pm 1.80$ in 1990; Mann-Whitney, $P > 0.05$) or in the estimated ratios of kids to older animals ($0.217 \pm .036$ and $0.265 \pm .041$ yg/ad, respectively; t test for Ratio Estimators, $P > 0.05$, Cochran 1977) between the censuses.

TABLE 2. Number of mountain goats counted in seven areas of the Olympic Range during July 1983 and 1990 censuses. Numbers represent actual counts and were not adjusted for sightability.

Area	1983	1990
Klahhane	52	2
Dana-Wilder	45	3
Chimney	52	35
Royal Basin	36	0
Constance/Charlia	65	24
Buckhorn	33	11
Pershing/Washington	13	8

Relative contributions to the apparent decline in goat numbers by the NPS removal program or other forces are unclear, and are considered in detail elsewhere (Houston *et al.* 1991). Known goat removals totaled 326 animals from autumn 1983 through autumn 1989 [245 (75.2%) removed by NPS, 80 (24.5%) legally harvested outside the park, 1 (0.3%) illegally killed in the park]. Annual removals were highly variable ($\bar{X} = 46.6 \pm 34.7$ goats/year, range 8-91), and would have averaged about four percent of the estimated 1983 population.

However, such summary calculations may be misleading because: (1) removals were not distributed across the population in relation to goat densities, but were sometimes concentrated on particular subpopulations (Houston *et al.* 1991), (2) NPS removals could have been effectively greater than the totals indicate. In relation to subpopulations (point 1), NPS removals were probably the force driving the decline of the Klahhane Ridge goats (Table 2, 43 animals removed 1984-89), but even there goat numbers continued to decline when removals were discontinued from 1985 to 1987 (Houston and Stevens 1988). Similarly, park removals probably contributed to substantial declines at Dana-Wilder (43 goats removed 1983-89) and Royal Basin (14 removed).

In relation to the effectiveness of removals (point 2), aerial darting and net gunning were used to capture goats from 1985-1989 (Houston *et al.* 1991); only rarely were kids captured with these techniques during the July (primarily) operations. About 66% of the 102 adult females captured were lactating, and we suspect that few of their kids, if any, survived. Moreover, some yearlings may continue to depend heavily on maternal females (Hutchins 1984). Consequently, the population effects of NPS removals were likely somewhat greater than indicated.

Still, the indicated population declines seem disproportionate to the removals imposed in several other areas of the park. For example, Stevens (1983) estimated the Mt. Appleton subpopulation at about 35-60 goats in 1980, and 46 were counted during the 1983 census. However, only 13-21 goats were recorded during 4 subsequent censuses from 1984-1986 (the area was not drawn for census in 1990). Eleven animals were removed (9 in 1988). By 1989, no goats, or their sign, were observed during the removal program despite three aerial searches. We suspect that substantial winter mortality may have affected this, and other, subpopulations as winter snowpack returned to more "normal" levels, following unusually low levels from about 1976 to 1981 (Stevens 1983). Such patterns are not unusual for mountain goats: Smith (1984), for example, documented strong density-independent mortality among goat populations in southeast Alaska during severe winters.

Mountain goats in the Olympic Range appear to have declined considerably from 1983-1990, but the large standard errors for overall population size (and for Klahhane Ridge—a major subpopulation, Houston and Stevens 1988) makes us wary of proposing detailed "explanations" for these changes. Park managers, moreover, should recognize that the uncertainty associated with the population estimate translates directly to uncertainty in the scale of removal efforts required in the future.

Alien species, such as goats in the Olympics, pose special management problems for national parks because they often disrupt established biological processes. Few people appreciate the scale of this problem: In a 1980 report to Congress 300 NPS areas reported 602 "threats" to natural

resources that involved alien plants and animals (NPS State of the parks–1980). Threats were particularly severe in the Hawaiian parks. Introduced mammals have been surprisingly difficult to control, due in part to their versatile life history patterns and to an increase in political, economic, and social concerns. It remains to be seen if the NPS will receive the required support for control of alien mammals as public awareness increases on the value of conserving the natural biotic diversity in national parks.

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Serologic, Parasitic and Pregnancy Survey of the Colockum Elk Herd in Washington

Abstract

This study was undertaken to determine the prevalence of selected infectious and parasitic diseases and to compare pregnancy diagnostic techniques in the Colockum elk herd. Between January 1988 and March 1990, 64 Rocky Mountain elk (*Cervus elaphus nelsoni*), less than one year old to maturity, were captured on winter range of the Colockum region in Central Washington. Serum antibody titers to bovine respiratory syncytial virus (RSV), infectious bovine rhinotracheitis (IBR), parainfluenza-3 virus (PI-3), *Hemophilus*, and *Campylobacter* from 45 elk were low or insignificant. All samples were seronegative for brucellosis and leptospirosis. Rectal palpation of cows of reproductive age (>1½ years, n = 24) was performed to detect pregnancy, and serum from those cows was tested for pregnancy specific protein B (PSPB). Twenty-two cows tested positive for pregnancy specific protein; whereas 21 of those cows tested positive on rectal palpation. No female calves (n = 3) or males (n = 13) tested positive for PSPB. Based on fecal sample analysis, 36 of 46 (78%) elk were negative for internal parasites while the remaining had low parasite egg, oocyst or larvae numbers. The significance of these results is that the Colockum elk have low prevalence of selected infectious diseases, few internal parasites, and PSPB compares favorably with rectal palpation for pregnancy diagnosis.

Introduction

The Colockum Elk Study, a five year project, was started in July 1987 to map and inventory elk habitat, determine distribution and migration patterns of elk, determine the prevalence of parasites from fecal analysis, selected infectious diseases from serologic testing, and compare pregnancy testing methods of cows. This report details the results of infectious disease, internal parasite, and pregnancy method testing. There have been no such previous studies performed on elk in the Colockum herd.

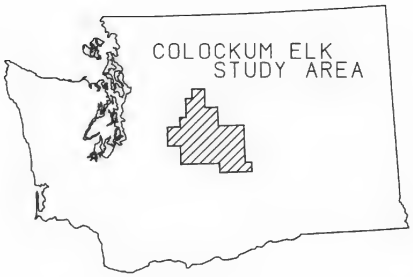
The infectious diseases and internal parasites for which the elk were tested are common pathogens in cattle which may be of clinical and economical significance (Blood *et al.* 1989). There have been no challenge inoculation studies with RSV, IBR, PI-3, or *Hemophilus* in elk. *Campylobacter*, a very ubiquitous bacterium, has been reported to cause increased fetal deaths and low fawn production in Wyoming antelope; however, this has not been noted in elk (Thorn *et al.* 1982). *Brucella*, an abortifacient, has been well documented in elk. The most prevalent signs include abortion, premature birth or birth of weak nonviable calves. Currently, brucellosis in elk is restricted to the Yellowstone ecosystem and has not been reported in elk from Washington. Clinical BVD and leptospirosis have not been reported in elk.

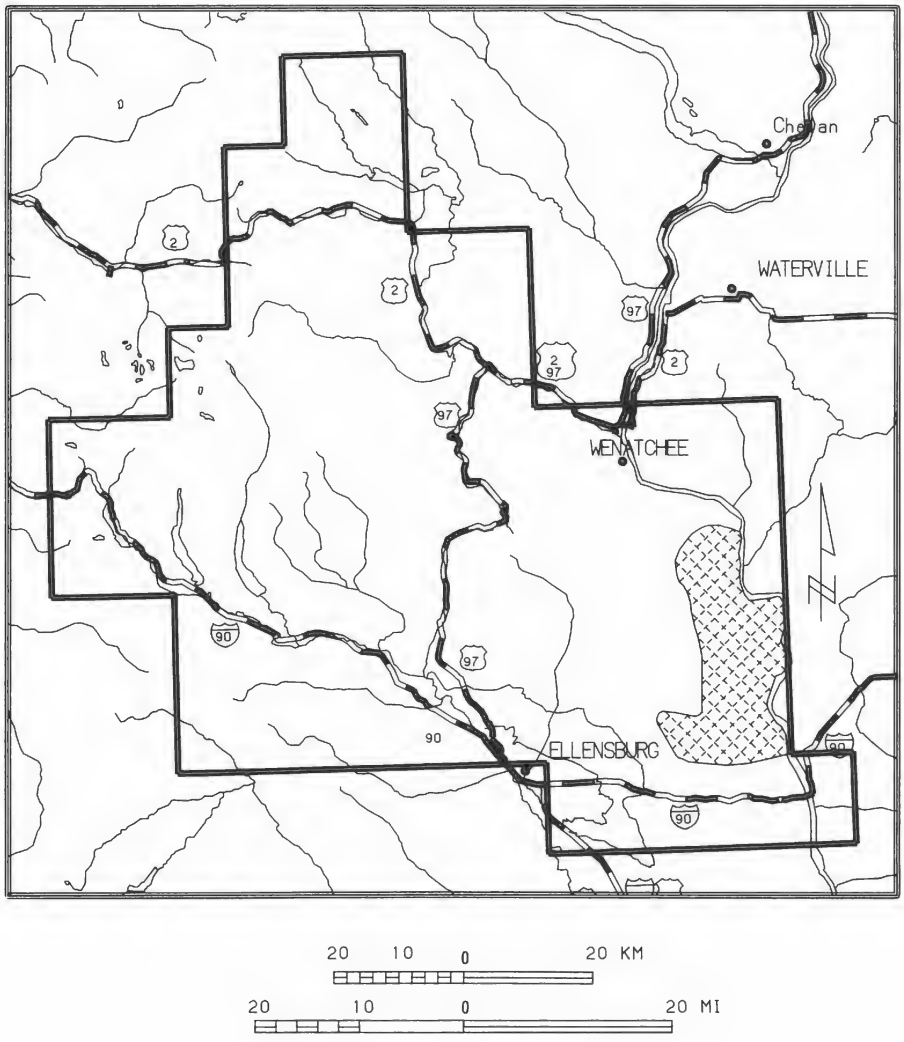
Description of Study Area

The Colockum Study area encompasses approximately 2,400 Km^2 (Figure 1) in Central Washington. The Washington Department of Wildlife Colockum Wildlife Area is centrally located in the study area. The primary study area is an eastern slope of the Cascade Mountain Range generally bordered to the east by the Columbia river and to the south and west by the Kittitas valley. Colockum rangeland varies from shrub steppe to coniferous forest with altitude ranging from 175 to 1980 m. Annual precipitation is 15-76 cm. Timber, livestock, mining, irrigation and hydroelectric watershed, winter sports and outdoor recreation are important industries and activities in the region. Elk are the primary ruminants in the area. Other ruminants include cattle, domestic sheep, mule deer, domestic and mountain goats, and a small population of captive bison.

Indian pictographs in the Colockum region suggest elk were native to the area; however, few or no elk were noted by white settlers in the mid- to late-nineteenth century (Dow 1964). Herd ancestors were transplanted in 1913 and 1916 from Yellowstone National Park. The current prehunting

Figure 1. The Colockum Elk Study area in Central Washington (right). Capture site area (shaded) within the Colockum Elk Study area (below).





season population is approximately 6,500 and accounts for 10% of the annual bull harvest for Washington.

Materials and Methods

Elk were captured by four techniques: 1) portable panel trap, 2) permanent corral trap, 3) net gunning from a helicopter, and 4) darting with immobilizing drugs from a helicopter. Fifty-one elk were examined by a veterinarian (Hein) at the time of capture.

The portable panel trap (2.5 m high x 2.5 m wide x 5 m long) was used in January 1988 and 1989. It was baited with alfalfa hay and salt and equipped with a trip wire. The figure eight corral traps (2.5 m high x 23 m diameter and 2.5 m high x 6 m diameter), used in January 1988, were baited in a similar manner. In both the panel and corral traps, an intramuscular injection of succinycholine at a dosage of 15-20 mg per elk via darts fired from a Palmer Cap-Chur® dart gun was used for immobilization. A 3.3 x 3.3 m net fired from a Coda® net gun from a Hughes 500 helicopter was used in February 1988 and 1989. Due to trauma to the elk and possible human injury, this method of capture was discontinued.

Elk were also darted in February 1989 and 1990 with Palmer Cap-Chur® darts from the same helicopter with a combination of xylazine (Rompun®) at a dosage of 20-70 mg per elk and carfentanil (Wildnil®) at a dosage of 1.5-3.6 mg per elk. One elk was darted with 70 mg xylazine and 8.6 mg etorphine (M99®). Reversal of carfentanil and etorphine in the narcotized elk was accomplished with naloxone at dosages of 140-260 mg. One-third of the naloxone was administered subcutaneously while the remainder was given intravenously. Recycling of the narcotics was observed.

Blood was collected from the jugular vein, allowed to clot, centrifuged, and the serum was collected and frozen prior to shipment for analysis. Serum samples were analyzed by the Washington Animal Disease Diagnostic Laboratory (WADDL), Washington State University, Pullman, Washington. Antibody against bovine respiratory syncytial virus (RSV), infectious bovine rhinotracheitis (IBR), bovine virus diarrhea (BVD), and parainfluenza-3 virus (PI-3) was tested by microtiter virus neutralization (Dunbar *et al.* 1985; Foreyt and Everman 1988). Serum antibody titers to *Hemophilus, Campylobacter,* and *Leptospira* were determined by microtiter agglutination, and *Brucella* was tested by latex agglutination.

Fecal samples were analyzed for parasite eggs, oocysts, and larvae at the Department of Microbiology and Pathology, College of Veterinary Medicine, Washington State University. Prior to shipment, fecal samples were stored at 4°C. Fecal flotation with a standard sugar flotation technique (sp. gr. = 1.27) was used to determine the numbers of gastrointestinal parasite eggs and coccidia oocysts. A Baerman apparatus technique was used to evaluate feces for first stage larvae of lungworms.

Serum was assayed for pregnancy specific protein B (PSPB) at the Department of Animal Science, College of Agriculture, University of Idaho, Moscow, Idaho. Forty samples (13 male; 3 calf, 2 yearling and 22 adult female) were assayed for PSPB by the radioimmunoassay procedure (Sasser *et al.* 1986). Field pregnancy determination was by rectal palpation of fetal membranes, uterine cotyledons, or fetal ballottement.

Results and Discussion

Five elk were captured in the portable panel trap, 17 in the figure eight corral trap, 18 by net gunning from a helicopter, and 24 by darting from a helicopter. Captured elk represented less than one percent of the herd population. Ideally, 10 percent of the population should have been tested, but this was not possible due to fiscal limitations. All elk were in good physical condition except one cow that was very thin. No other elk exhibited signs of clinical disease.

Neutralizing antibody titers to RSV in this study ranged 1:5 to 1:80 (median = 1:7.5) and were detected in 6 of 45 (13%) elk (Table 1). The low seroprevalence indicates RSV infection is not widespread within the elk tested. Serum titers to IBR of 1:5 to 1:10 (median = 1:5) were found in 17 of 45 (38%) elk indicating low incidence of exposure without observed clinical manifestation. All elk except a mature bull tested negative to BVD. A titer of 1:40 in the bull indicated exposure, but no clinical disease was observed when the bull was handled. Serum titers to PI-3 were found in 30 of 45 (67%) elk and ranged 1:5 to 1:160 (median = 1:15). These titers indicate widespread exposure. *Hemophilus* titers were present in 43 of 46 (96%) elk, ranging from 1:50 to 1:512 (median = 1:128). These titers reveal widespread

TABLE 1. Serologic results for assays against respiratory syncytial virus (RSV), infectious bovine rhinotracheitis (IBR), bovine virus diarrhea (BVD), parainfluenza-3 virus (PI-3), *Hemophilus*, *Campylobacter*, *Brucella*, and *Leptospira* in the Colockum elk of Central Washington.

			Calves		Yearlings		Adults	
			Antibody Titers[a]					
Infectious Disease	Total Positive/ Total Tested	Percent Positive	Male (n = 4)	Female (n = 3)	Male (n = 4)	Female (n = 3)	Male (n = 8)	Female (n = 23)
RSV	6/45	13	Neg	Neg	Neg	Neg	5-40 (n = 3)	5-80 (n = 3)
IBR	17/45	38	Neg	Neg	Neg	Neg	5-10 (n = 2)	5-10 (n = 15)
BVD	1/45	2	Neg	Neg	Neg	Neg	40 (n = 1)	Neg
PI-3	30/45	67	Neg	20 (n = 1)	5-10 (n = 2)	5-40 (n = 2)	10-160 (n = 6)	5-160 (n = 19)
Hemophilus	43/45	96	64-512 (n = 4)	128-512 (n = 3)	128-512 (n = 4)	128-512 (n = 3)	50-128 (n = 8)	50-512 (n = 21)
Campylobacter	45/45	100	25-50 (n = 4)	50-100 (n = 3)	25-100 (n = 4)	50-200 (n = 3)	25-100 (n = 8)	25-100 (n = 23)
Brucella	0/45	0	Neg	Neg	Neg	Neg	Neg	Neg
Leptospira	0/45	0	Neg	Neg	Neg	Neg	Neg	Neg

[a]Numbers indicate reciprocal serum titer values from positive animals.

exposure. All elk had positive antibody titers to *Campylobacter*, ranging from 1:25 to 1:200 (median = 1:50). A titer of 1:200 in one elk reflects recent exposure; however, without additional samples the titer is difficult to interpret. Antibody tests for *Brucella* and *Leptospira* were negative. Both diseases are important diseases of livestock, but at this time it does not appear that the Colockum elk are a reservoir of infection for livestock that are sympatric.

Numbers and counts of internal parasite ova detected are listed in Table 2. *Nematodirus* sp., the thinnecked intestinal worm, was found in 7 of 46 (15%) elk. Eggs per gram of feces ranged from 2-14 (median = 5). *Trichuris* sp., the whipworm, was found in 5 of 46 (11%) elk. Egg counts were low, ranging from 1-6 (median = 4). One *Eimeria* sp. oocyst was found in one elk. Tapeworm eggs of the genus *Moniezia* were found in 3 of 46 (7%) elk. Egg counts ranged 12 to 18 (median = 15). Trichostrongyle stomachworm (*Hemonchus*, *Trichostrongylus*, *Ostertagia*) eggs were found in one elk with the count of eight eggs per gram. First stage larvae of lungworms were not present in any samples.

Rectal palpation for determination of pregnancy in 2 yearlings and 22 adult cows indicated that 21 of the adults were pregnant. Serum PSPB results (Table 3) and rectal palpation results of adult cows were in full agreement. Of the two yearling cows, one tested positive for PSPB whereas the result for the other was inconclusive. Both of the yearling cows tested negative on rectal palpation. These inconsistencies may be explained by an error on rectal palpation or persistence of PSPB in circulation after recent fetal death as seen in red deer (Haigh *et al.* 1988). Based on rectal palpation, conception rate for adult cows was 95% and for yearling and adults combined was 88%. All 13 male elk and 3 female calves tested PSPB negative. The PSPB assay has also been used in deer (Wood *et al.* 1986) and mountain goats (Houston *et al.* 1986) with reliable results.

Conclusions

Based on this study, elk in the Colockum herd were physically healthy. Only one adult cow appeared in poor physical condition and on rectal palpation a large abdominal mass which may have been a tumor was detected. None of the other captured elk exhibited signs of disease. Evaluation of serum

TABLE 2. Results of fecal analysis *Nematodirus* (thinnecked intestinal worm), *Trichuris* (whipworm), *Eimeria* (coccidia), *Moniezia* (tapeworm), trichostrongyles (stomach worms), and lungworms in the Colockum elk herd in Central Washington.

		Calves		Yearlings		Adults	
Parasite	Total Positive/ Total Tested	Male (n = 4)	Female (n = 3)	Male (n = 4)	Female (n = 3)	Male (n = 8)	Female (n = 24)
Nematodirus	7/46	2-8* (n = 3)	10-14 (n = 2)	4 (n = 1)	0	0	3 (n = 1)
Trichuris	5/46	1-6 (n = 2)	4 (n = 1)	1-4 (n = 2)	0	0	0
Eimeria	1/46	1 (n = 1)	0	0	0	0	0
Moniezia	3/46	18 (n = 1)	12-25 (n = 2)	0	0	0	0
Trichostrongyles	1/46	0	0	0	0	0	8 (n = 1)
Lungworms	0/46	0	0	0	0	0	0

*Values expressed are ranges of numbers of eggs, oocysts, or larvae per gram feces in positive elk.

TABLE 3. Comparison of pregnancy specific protein B (PSPB) and rectal palpation results for pregnancy determination in the Colockum elk herd in Central Washington.

Age	Sex	No. of Animals	PSPB+	PSPB−	Rectal+	Rectal−
All ages	Male	13	0	13	ND[a]	
Calves	Female	3	0	3	ND	
Yearlings	Female	2	1	In[b]	0	2
Adult	Female	22	21	1	21	1

[a]ND = Not done

[b]In = Inconclusive

titers indicated low values or low rates of infection for ruminant respiratory, intestinal or reproductive pathogens. All elk tested negative for *Leptospira* and *Brucella*. Analysis of feces revealed low level infestation with parasites found commonly in ruminants. The PSPB serum assay appears to be an excellent test for mid-term gestation determination in elk. It correlated well with pregnancy results by rectal palpation.

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Differences in the Distribution of Adult and Immature Bald Eagles at an Autumn Concentration in Montana

Abstract

During the autumns of 1983 and 1984 we compared the relative abundance of adult and immature Bald Eagles (*Haliaeetus leucocephalus*) at two foraging sites along Lower McDonald Creek in Glacier National Park, Montana. The ratio of adults to immatures differed between the locations. The proportion of adults was higher during both years at a public viewing area compared to a site 1 km downstream in an area closed to public access. We examined four hypotheses related to migration timing, human disturbance, behavioral exclusion, and food availability that could account for these differences. There were temporal differences in adult and immature migration, but they were insufficient to explain age-ratio dissimilarities at a given time. The ratio of adults to immatures did not change in response to the number of people at the public viewing area. Adults displaced immatures from perch sites and food less frequently than expected. Live salmon were more abundant at the public viewing area, but the downstream site had greater opportunity to scavenge accumulated carcasses. Our results suggest that food availability was the primary factor influencing the distribution of adult and immature eagles during this study.

Introduction

The spatial distribution of adult and immature Bald Eagles (*Haliaeetus leucocephalus*) often differs among and within geographic locations (Hancock 1964, Stalmaster and Newman 1978, Fisher *et al.* 1981, LaBonde 1981, Fisher and Hartman 1982, Millsap 1986). Several explanations of age-related differences in distribution have been suggested, but data have been insufficient to test specific hypotheses.

We compared the ratio of adult to immature Bald Eagles at two locations along Lower McDonald Creek (LMC) during the autumns of 1983 and 1984 in Glacier National Park, Montana. We then examined differences in these ratios with respect to four hypotheses: age-related differences in the distribution of Bald Eagles results from (1) *migration timing*—adult and immature Bald Eagles differed in their arrival or departure dates at the concentration (Sprunt and Ligas 1966, Steenhof 1976, Fitzner and Hansen 1979); (2) *human disturbance*—dissimilar response of adults and immatures to human presence (Stalmaster 1976, Stalmaster and Newman 1978); (3) *behavioral exclusion*—aggressive interactions between adult and immature Bald Eagles resulted in a greater degree of exclusion of immatures from one site (Fisher and Hartman 1982, Craighead 1979); and (4) *food availability*—adult and immature eagles responded differently to the quantity, quality, and accessibility of food (LaBond 1981, Fisher *et al.* 1981).

Study Area

Glacier National Park is adjacent to the Canadian border in northwestern Montana and is the United States' portion of Waterton-Glacier International Peace Park. Each autumn in recent years several hundred migrating Bald Eagles have been attracted to LMC to feed on spawning kokanee salmon (*Oncorhynchus nerka*) (McClelland 1973, Shea 1978). LMC flows 4 km from the outlet of Lake McDonald to the confluence with the Middle Fork of the Flathead River. The average creek width during autumn is approximately 25 m. The creek generally ranges from 10 to 60 cm deep and is interspersed with deeper pools and riffles. Salmon spawning occurs in shallow areas (<20 cm) with gravel beds.

Vegetation along LMC consists of black cottonwood (*Populus trichocarpa*), riparian shrubs, and mixed coniferous forest. Plant species composition along the creek was described in detail by Habeck (1970).

Methods

During the autumns of 1983 and 1984, weekly counts of all Bald Eagles at LMC were conducted in accordance with the procedures described by McClelland *et al.* (1982). Eagles with a predominantly white head and tail were classified as adults and all others as immatures. We

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conducted site-specific counts of adult and immature Bald Eagles from 10 October through 20 November 1983 and from 20 October through 1 December 1984. Counts were conducted 4 d per week at 2 locations along LMC: Apgar Bridge and the oxbow blind (Figure 1). Apgar Bridge was a public viewing area where >2500 people viewed Bald Eagles on some autumn days. The oxbow blind was approximately 1 km downstream from Apgar and within an area closed to the public during the eagle concentration. The blind, used for observations at the oxbow, had a covered walkway which allowed entry without disturbing eagles. The differences in dates of our surveys between the two years reflects the dates that eagles were present at LMC.

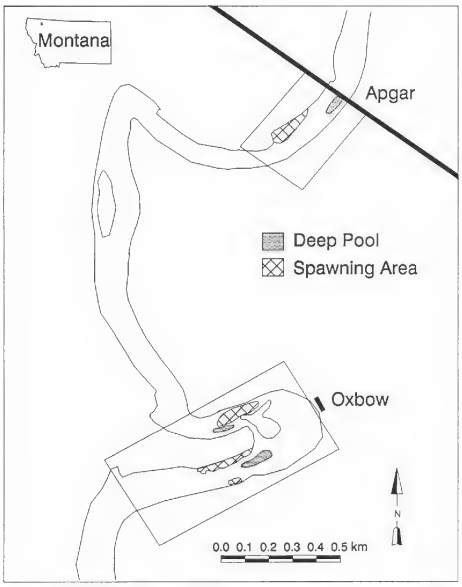

Figure 1. Lower McDonald Creek showing the areas visible from Apgar Bridge and the Oxbow Blind (rectangles). Deep pools used by salmon for staging and salmon spawning areas are shown for each observation area.

Because eagles moved throughout the day, 2 to 4 censuses were conducted each day with a minimum of 2 h between censuses. The 2 h minimum was based on prior sampling (during 1983) in which no eagles remained at a given perch longer than 1.5 h (pers. observ.). Observation of 114 wing-marked and 57 transmitter-equipped Bald Eagles at LMC over a 10 yr period also revealed that individuals seldom remained in the same location longer than 2 h (pers. observ.). Although we felt that 2 h was sufficient to avoid double-counting eagles at the same location, we could not be certain that samples were independent because all individuals were not marked.

The white head and tail of adult Bald Eagles makes them more conspicuous than subadults against a dark background (e.g., foliage), thereby affecting adult to immature ratios (Hancock 1964, Joseph 1977, Stalmaster and Newman 1979, Pannetier 1980, LaBonde 1981). This bias would be most pronounced for surveys done quickly, from a distance, or while moving (e.g., aerial surveys). Our sampling was done from stationary vantage points in proximity to the eagles (<200 m) and with spotting scopes. Consequently, we assumed that detectability bias did not influence our results.

We partitioned each season into three equal time periods (early, mid, and late season) to assess whether the proportions of adult and immature eagles differed during the 1983 and 1984 seasons. We used chi square tests of independence to test the association between age and location for each season and year.

Prey abundance was estimated bi-weekly by two Montana Department of Fish, Wildlife and Parks (MDFWP) biologists. While snorkeling, they independently estimated the number of live salmon at each riffle and pool and these estimates were averaged for a final count. We used two-way analysis of variance, blocked by survey date, to test for differences between observers and location. Salmon abundance prior to October of each year was excluded from this analysis because the fish were still moving upstream and migrating Bald Eagles had not arrived by this time.

A displacement attempt was defined as an eagle attempting to supplant another eagle from its perch site or food. Only successful perch-site displacements were recorded because it often was difficult to distinguish an attempted perch-site displacement from simply perching proximal to another eagle. To compare the frequency of aggressive encounters between adult and immature eagles we used the procedure described by Hailman (1975) (see also Griffin 1981), which derives expected values of a chi square goodness-of-fit test by using relative abundance of each age class. We used the overall proportion (combined counts) of each age class at each location during each year to derive expected values.

We recorded all foraging attempts observed during 2-hour time periods conducted 3 times per d, 4 d per week during each year. The morning observation period each day began 30 min after sunrise. An evening observation period ended 30 min before sunset, and a mid-day period was evenly arranged between the morning and evening periods. Observation periods alternated between locations. For each foraging attempt observed we recorded the age class of the eagle and the foraging method used. Each attempt was assigned to 1 of 3 foraging methods: stooping, piracy, or scavenging.

In 1986 we examined whether the proportion of adults to immatures changed in response to the number of people at Apgar Bridge. From 27 October through 9 November we recorded the number of adult and immature eagles at Apgar and the number of people present at the viewing area at 2-hour intervals throughout each day. We used Spearman's rank correlation for this analysis.

Results

During 1983 we conducted 33 censuses at Apgar and 36 at the oxbow. The mean number of eagles per census was 14.6 ± 9.1 SD at Apgar and 8.5 ± 5.3 SD at the oxbow. During 1984 we conducted 82 censuses at Apgar and 86 at the oxbow. The mean number of eagles per census was 19.9 ± 12.9 SD at Apgar and 21.4 ± 14.2 SD at the oxbow. Overall (combined locations), adults comprised 63 percent and 67 percent of the total population during 1983 and 1984, respectively. The proportion of adults was higher at Apgar and lower at the oxbow during both 1983 ($X^2 = 289.8$, $P < 0.001$, 1 df) and 1984 ($X^2 = 330.9$, $P < 0.001$, 1 df). This relationship also persisted within each period of the season during 1983 ($X^2 = 130.65$, $P < 0.001$, 1 df; $X^2 = 93.96$, $P < 0.001$, 1 df; and $X^2 = 69.11$, $P < 0.001$, 1 df, early, mid, and late seasons, respectively) and 1984 ($X^2 = 9.80$, $P = 0.002$, 1 df; $X^2 = 80.29$, $P < 0.001$, 1 df; and $X^2 = 225.23$, $P < 0.001$, 1 df, early, mid, and late season, respectively) (Table 1).

Migrating adult and immature Bald Eagles are not synchronous in their patterns of arrival and departure at LMC in some years. The number of immatures tends to peak earlier than adults. The number of adults often increases and then decreases more rapidly, and within a shorter time period, than the number of immatures (McClelland *et al.* 1982) (Figure 2).

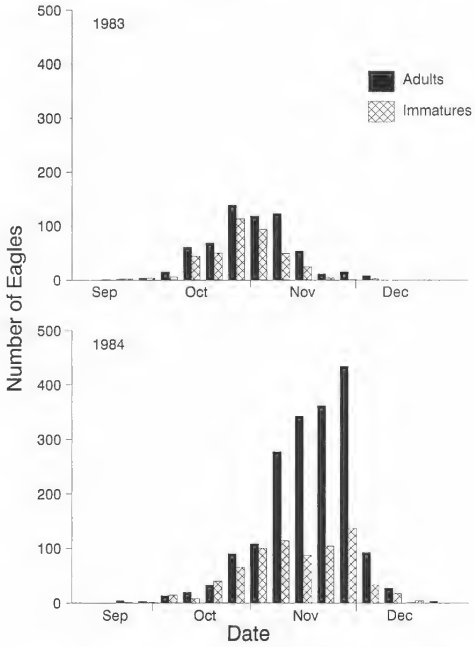

Figure 2. Weekly censuses of adult and immature Bald Eagles along LMC during the 1983 and 1984 concentration periods.

TABLE 1. The number (percent) of adult land immature Bald Eagles counted at Apgar and Oxbow during ealry, mid, and late season of 1983 and 1984.

	Early		Mid		Late		Total	
	Apgar	Oxbow	Apgar	Oxbow	Apgar	Oxbow	Apgar	Oxbow
1983								
Immatures	20 (11)	144 (68)	66 (19)	144 (56)	30 (18)	76 (68)	116 (17)	364 (63)
Adults	162 (89)	68 (32)	290 (81)	112 (44)	134 (82)	36 (32)	586 (83)	216 (37)
1984								
Immatures	2 (9)	28 (47)	10 (12)	164 (68)	44 (9)	300 (53)	56 (10)	492 (57)
Adults	20 (91)	32 (53)	76 (88)	78 (32)	432 (91)	264 (47)	528 (90)	374 (43)

During our 1986 study the number of people at Apgar at a given time ranged from one (the observer) to 205 ($\bar{x}$ = 38.7, ± 48.0 S.D.; n = 63). The ratio of adult to immature eagles was not significantly correlated with the number of people present (Spearman r = −0.16, P = 0.21).

The frequency of perch-site displacements by immature and adult eagles did not occur in proportion to the relative abundance of each age class in 1983 at the oxbow (X^2 = 15.32, P < 0.001, df = 1, n = 84), 1983 at Apgar (X^2 = 13.31, P = 0.004, 1 df, n = 72), 1984 at the oxbow (X^2 = 29.65, P < 0.001, 1 df, n = 74), or in 1984 at Apgar (X^2 = 118.77, P < 0.001, 1 df, n = 109). In all cases immatures initiated successful displacements against adults in frequencies greater than expected (Figure 3). Conversely, adults initiated successful perch-site displacements against immatures less frequently than expected in 3 of 4 cases.

A small sample size (n = 8) precluded an analysis of food displacements during 1983. During 1984 the frequencies of food displacements by immatures and adults was not proportional to their relative abundance at Apgar (X^2 = 190.40, P < 0.001, df = 1, n = 67); however, this difference was not detected at the oxbow (X^2 = 2.52, P = 0.472, 1 df, n = 83). The pattern of food displacements was similar to perch-site displacements; immatures initiated displacements more frequently than expected against adults (Figure 4). The success of food displacements also was not dependent on age (X^2 = 1.07, P < 0.1, 1 df).

Salmon, the nearly exclusive food source of Bald Eagles at LMC, were consistently more abundant at Apgar than at the oxbow during both 1983 and 1984 (Figure 5). Estimates of salmon abundance did not differ between observers (F = 0.03, P = 0.86), but differed significantly between locations (F = 26.7, P < 0.001) and among dates (F = 5.25, P < 0.001). Since 1979, when biweekly salmon counts began, a staging pool at Apgar consistently supported the highest number of salmon in LMC (J. Fraley, pers. comm.).

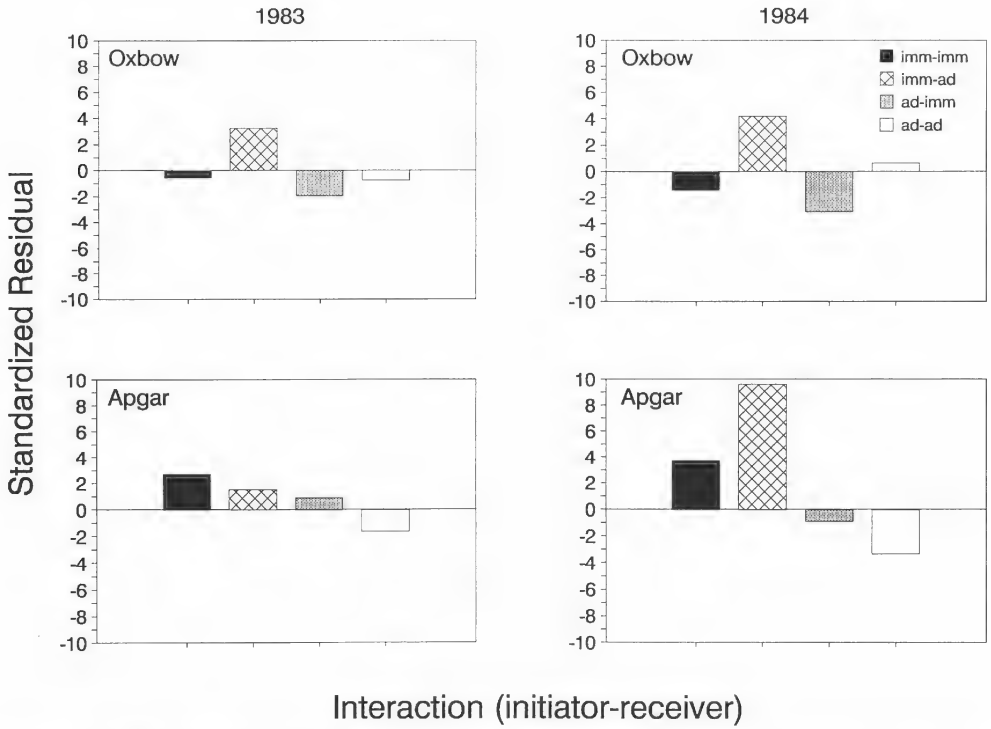

Figure 3. Standardized residuals (Haberman 1973) from chi square goodness-of-fit test of perch-site displacements between immature and adult Bald Eagles during 1983 and 1984 at the oxbow and Apgar.

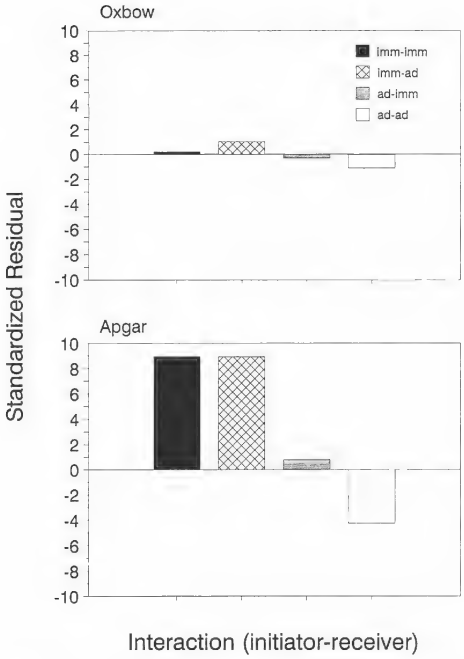

Figure 4. Standardized residuals (Haberman 1973) from chi square goodness-of-fit test of food displacements between immature and adult Bald Eagles during 1984 at the oxbow and Apgar.

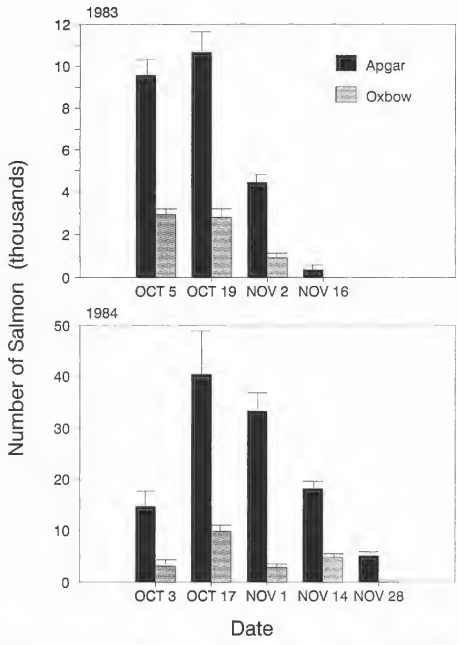

Figure 5. The average number of salmon counted at Apgar and the oxbow during 1983 and 1984. Crossbars represent the high count of the two observers (the range).

Kokanee salmon weakened and died within 2 to 3 weeks after spawning at LMC (pers. observ.). Although surveys of salmon abundance were of live salmon, differences in carcass accumulations between locations were apparent. Because of the relatively straight stream course at Apgar, dead salmon accumulated primarily in deep pools and were unavailable to eagles. At the oxbow, however, dead salmon accumulated in the relatively shallow backwater or along the shoreline.

Foraging methods were age dependent during 1984 ($X^2 = 121.4$, $P < 0.001$, 2 df). Adults stooped more frequently than expected and immatures scavenged and pirated more frequently than expected. In 1983 we had an insufficient sample for statistical analysis.

Discussion

Differences in migration timing clearly influenced the adult/immature ratio during each season. However, our surveys were conducted throughout the entire season and consistently higher proportions of adults at Apgar and immatures at the oxbow persisted. Therefore, we rejected the hypothesis that migration timing accounts for the age-related distribution differences at LMC. These results do, however, illustrate that timing can greatly influence the results of surveys.

Adult Bald Eagles are more sensitive than immatures to human activity (Edwards 1969, Shea 1973, Stalmaster 1976, Stalmaster and Newman 1978, Fisher and Hartman 1982). Because of the high level of human activity at Apgar (sometimes >2500 people per day), we predicted that adult Bald Eagles would avoid Apgar if human disturbance were a primary influence on distribution. Adult Bald Eagles, however, were found in higher proportions than immatures at Apgar.

We offer 2 explanations for the adult's failure to avoid Apgar. First, eagles may have become habituated to people at Apgar where visitors have been restricted to a viewing area (McClelland 1981) (see also Grier 1969, Edwards 1969, Stalmaster and Newman 1978, Russell 1980,

Hansen *et al.* 1984, Harmata 1984). However, the process of habituation needs further testing (Knight and Knight 1984). Secondly, the highest concentration of food on LMC was at Apgar. This may have outweighed the effect of disturbance (see also Knight 1981, Skagen 1981); however, this hypothesis has not been tested.

Behavioral exclusion implies an influence on distribution when "dominant" eagles exclude "subordinate" eagles from preferred areas. Some researchers have reported that adult Bald Eagles are dominant over immatures (e.g., Lish 1973, Stalmaster and Gessaman 1984); others have shown that size is a more important determinant of dominance than age (Hansen 1986, Knight and Skagen 1988). We predicted that if dominance were age-related, adult Bald Eagles would exclude immatures from preferred areas. Griffin (1981) also suggested that conditioning from previous encounters could encourage a dominant-subordinant relationship favoring adults. Neither our prediction nor Griffin's suggestion were supported at LMC. Our data showed that immatures successfully displaced adults from both perch sites and food more often than the reverse. Additionally, eagles that were displaced from perch sites or food seldom left the area, but more often returned to a nearby perch site. It is possible that behavioral exclusion may influence distribution at other locations, under conditions different than those depicted in our study, or is based on attributes other than age (e.g., size). Our data, however, do not support behavioral exclusion as an important influence on age-related distribution at LMC.

Food availability may have an important influence on the distribution of wintering Bald Eagles and may differentially influence the distribution of adult and immature eagles (Stalmaster *et al.* 1979, Fisher *et al.* 1981). Stalmaster (1976), LaBonde (1981), and Fielder and Starkey (1987) suggested that immature eagles were found in greater proportion in areas where food was more abundant and accessible. This leaves unanswered why adults in these areas did not concentrate at these "abundant and accessible" food sources since through greater experience they presumably would have been more aware than immatures of these locations.

We suggest that the type or condition of food may have major influence on its availability to Bald Eagles. Immatures are less effective at capturing live prey and may be more dependent than adults on scavenging or piracy (Shea 1973, Sherrod *et al.* 1976, Joseph 1977, Fisher and Hartman 1982, Harmata 1984). Our data at LMC were consistent with these reports: adult Bald Eagles stooped more frequently than expected and immatures scavenged and pirated more frequently than expected. The opportunities for immatures to scavenge carcasses in the shallow waters of the oxbow may have been more attractive than the more abundant, but more difficult to capture, live prey at Apgar.

We offer 3 explanations for the higher proportion of immatures at the oxbow: (1) adults seem to have little difficulty obtaining the more abundant live salmon at Apgar (i.e., scavenging was not necessarily easier for adults) (see also Shea 1973); (2) the energy content of salmon decreases as decomposition progresses (i.e., carcasses at the oxbow may be of lesser quality) (Stalmaster and Gessaman 1984); and (3) adults appeared much more reluctant than immatures to land on the ground. Given the opportunity, adults usually stooped on prey (carcasses or live salmon) rather than landing (see also Knight and Knight 1986). Wading often was necessary to take available carcasses at the oxbow.

Anecdotal evidence supporting the food availability hypothesis was found in a change of the age-class distribution of eagles following a loss of spawning habitat at the oxbow. A flood during 1975 resulted in diversion of the main flow of LMC away from the oxbow. The backwaters created by this diversion resulted in increased siltation, decreasing spawning habitat and numbers of salmon. Concomitantly, the proportion of adult Bald Eagles decreased at the Oxbow (pers. observ.).

In summary, our results suggest that food availability, particularly the condition of food, has an important influence on age-related distribution of Bald Eagles on LMC. Differences in migration timing occurred and influenced the overall ratio of adult to immature eagles, but was insufficient to explain why adult and immature Bald Eagles were distributed disproportionately between locations at any given time. Human disturbance and behavioral exclusion may be important influences on age-related eagle distribution in other areas or under different conditions. Our results, however, indicate that they were not important influences of distribution at LMC.

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Activity and Behavior of Free-Living *Sylvilagus nuttallii*

Abstract

A paucity of published information on activity and behavior of Nuttall's cottontail (*Sylvilagus nuttallii*) and of free-living leporids in general caused us to study these attributes in central Oregon in 1980-1981. Of 1,192 behavioral acts of free-living cottontails recorded between 1 hr before sunrise to 1 hr after sunset during 327.3 hr of observation from an elevated stand in March-August 1981, 92.9 percent were nonsocial and accounted for 92.6 percent of the time that cottontails were in view. Of time in view, cottontails spent 58.5 percent feeding, 23.0 percent resting, and 6.3 percent moving. Social behavior was observed among adults only during the reproductive season and accounted for only 7.4 percent of their activity budget. A bimodal pattern of daytime activity peaked 1-2 hr after sunrise and 0-1 hr before sunset. Activity of adult females was relatively constant seasonally, but adult males became extremely secretive after the reproductive season. Although no single environmental factor or group of factors was a significant determinant of activity in Nuttall's cottontail, the relatively solitary life-style and near absence of reproductive interactions during daylight hours may be behavioral mechanisms related to equitable division and conservation of available moisture.

Introduction

Knowledge of the biology of Nuttall's cottontail (*Sylvilagus nuttallii*), an endemic to the intermountain West (Hall 1981), is limited to descriptive accounts (Bailey 1936, Hall 1951, Ingles 1965, Janson 1946, Orr 1940) and to recent ecological studies in central Oregon (Hundertmark 1982, McKay and Verts 1978*a*, 1978*b*, Powers and Verts 1971, Skalski and Verts 1981, Verts *et al.* 1984) and British Columbia (Sullivan *et al.* 1989). Accounts of the behavior of this and other leporid species are based largely on scattered field observations or on observations of animals in pens or enclosures. The description and classification of behavioral patterns of the black-tailed jackrabbit (*Lepus californicus*) by Lechleitner (1958) remains the only detailed published account based on observations of free-living leporids. Herein, we categorize behavior, quantify relationships among various activities and environmental variables, and relate specific behavioral acts to ecology of Nuttall's cottontail in central Oregon.

Study Area and Methods

Field research was conducted on a portion of a 115.7-ha site approximately 5 km W Terrebonne, Deschutes County, Oregon (elevation, 835-842 m) used in several previous studies of *S. nuttallii* (Hundertmark 1982, McKay and Verts 1978*a*, 1978*b*, Powers and Verts 1971, Skalski and Verts 1981, Verts *et al.* 1984). The study area lies within 30 km of the western edge of the geographic range of *S. nuttallii* (Hall 1981). Climate is semiarid with hot dry summers and relatively cold winters; mean annual precipitation is 22.9 cm (U.S. Department of Commerce 1981). Vegetation in this section of the Columbia Basin Physiographic Province is most similar to the *Juniperus occidentalis/Artemisia tridentata-Purshia tridentata* association (Franklin and Dyrness 1973).

Field observations were conducted from early June-30 August 1980 and 7 February-30 August 1981 by systematic live trapping, ad libitum cruises, cruises during operation of traplines, and systematic observations by focal-animal sampling (Altmann 1974) from an elevated ($\approx$6 m) stand in a tree. In an effort to reduce bias in activity budgets related to differential ease of sighting individuals engaged in different behavior, the entire area observable from the stand was scanned until a cottontail was sighted, whereupon that individual was observed and its behavior recorded for 5 minutes; then, the area was scanned for additional cottontails for 5 minutes before observing and recording behavior of the previously sighted cottontail for another 5-minute period. The only deviation from this routine was when individuals interacted; interacting cottontails were observed until the interactions were complete or the cottontails were no longer in view.

Unbaited wooden box traps (15 X 19 X 58 cm) set in a 9- X 13-trap grid with approximately 90 m between traps were operated alternate weeks in June, 3 consecutive days each week in July, and daily 1-30 August in 1980. Traps also were operated 3 consecutive days during 3, 3, 2, and 4 weeks in April, May, June, and July, respectively,

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and daily 1-30 August in 1981. From 25 February to 3 March 1981, live traps were set at four sites within the study area chosen as potential areas for systematic behavioral observations. On the basis of the relative abundance of cottontails and of the physiognomy and vegetation that did not interfere greatly with observations of cottontails, one site ($\approx$6 ha) was selected. This report is based largely on the systematic observations conducted from a tree stand from which most of the $\approx$6-ha area was visible. All cottontails captured were marked with aluminum ear tags; weight, sex, and age (based on size, pelage, and reproductive status) for each cottontail were recorded. Cottontails captured also were marked for individual recognition by clipping guard hairs to form numerals along the flanks and dying the exposed underfur with Nynazol-D (females) or Rhodamine-B (males).

Initially, periods of 0.75-4.00 hr of observations from the stand were scheduled at all hours of the day and night during March-August 1981; however, observations were restricted to the period from 1 hr before sunrise to 1 hr after sunset when artificial light and a Star-tron night scope proved unsuitable for nighttime observations of Nuttall's cottontail. All subsequent observations were with the aid of 7 X 35 wide-angle binoculars. Because Lord (1961) reported that most activity of free-living eastern cottontails (*S. floridanus*) was before 0900 or after 1600, we sampled the interval between these hours less intensively.

During systematic observations from the elevated stand, time, location, identifying marks, and detailed descriptions of behavior were recorded on microcassette tapes and subsequently transcribed to field notes for all cottontails observed. The classification scheme devised for behavior of eastern cottontails and swamp rabbits (*S. aquaticus*) in enclosures (Marsden and Holler 1964) served as a framework for identifying and describing movements, postures, and other behavior exhibited by *S. nuttallii*. Site-and time-specific weather conditions were recorded before and after observation periods and cruises. Additional climatological data were obtained from records of the Redmond FAA AP weather station approximately 11 km S and 6 km E of the study area (U.S. Department of Commerce 1980, 1981). Data related to astronomical phenomena were obtained from the U.S. Naval Observatory (1979, 1980).

Coefficients of multiple correlation were computed for all combinations of activity and environmental variables. Data collected during observation periods were subjected to principal-component analysis; five dependent variables (total number, and number of adult, adult male, adult female, and juvenile cottontails observed/hr) and nine independent variables (date; time of day relative to sunrise or sunset; number of avian predators observed/hr; mean temperature, cloud cover, and windspeed during the period; number of consecutive days without precipitation; length of the previous night; index to lunar illumination during the previous night) were chosen for analysis based on correlation coefficients. Multiple regression was used to determine if principal components were related significantly ($P \leq 0.05$) to activity.

Results and Discussion

The Subjects

A minimum of 19 Nuttall's cottontails (individuals captured or observed) used the $\approx$6-ha site between 24 February and 30 August 1981. Among this group, 12 were adults: four marked females, six marked males, and at least one unmarked individual of each sex. If all 12 adults resided solely on the $\approx$6-ha area observable from the stand, population density of adults was $\approx$2/ha, approximately equal to the maximum density recorded on the Terrebonne Study Area during the preceding 8 years (Skalski and Verts 1981). Likely, several of these individuals included areas in their home range beyond the limits at which observations were recorded.

The Behavioral Repertoire

The 1,192 behavioral acts recorded during 327.3 hr of scheduled observations were classified initially into eight categories of posture and seven categories of movements, and these into 20 nonsocial and seven social behavioral patterns (Gehman 1984). The 27 behavioral patterns were combined into seven categories of nonsocial behavior (feed, rest, locomote, groom, tree-climb, interspecific interactions, and transitional acts) and two categories of social behavior (reproductive and nonreproductive). Nonsocial behavior accounted for 92.8 percent of the total number of acts observed and 92.6 percent of the total time that cottontails were in view (Table 1).

Of nonsocial behaviors, feeding accounted for the greatest proportion of the time during which

TABLE 1. Number and percent of total of each behavior observed, total and percent of total time each act was observed, and mean duration of each act for Nuttall's cottontail, Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Behavior Type and Behavior	Number Acts Observed	Percent of Acts Observed	Time Acts Performed (min)	Percent of Time Observed (min)	Mean Duration of Act (min)
Nonsocial					
Feed	303	25.4	2,202.8	58.5	7.27
Rest	163	13.7	863.9	23.0	5.30
Locomote	459	38.5	238.7	6.3	0.52
Groom	97	8.1	59.2	1.6	0.61
Tree-climb	47	3.9	114.2	3.0	2.43
Interspecific Interactions	15	1.3	7.5	0.2	0.50
Transitional Acts	23	1.9	1.8	0.1	0.08
Social					
Reproductive Interactions	77	6.5	261.0	6.9	3.39
Nonreproductive Interactions	8	0.7	15.0	0.4	1.88

S. nuttallii was observed (Table 1); 72.2 percent of feeding bouts were on grasses (principally *Bromus tectorum, Stipa thurberiana,* and *Sitanion hystrix*), 7.9 percent on juniper (*Juniperus occidentalis;* only in July and August), 1.0 percent on shrubs (flowers of green rabbitbrush, *Chrysothamnus viscidiflorus,* only), and 18.8 percent on unidentified plants. No cottontail was observed to feed on forbs.

Resting accounted for the next greatest proportion of the time during which cottontails were observed (Table 1). Nuttall's cottontails sat motionless in either an alert or hunched posture for 92.1 percent of the time they rested; they were in a lying position 6.9 percent of resting time and sprawled in a loafing posture 1.0 percent of resting time. One female was observed to sprawl in a loafing posture immediately after dusting on four occasions. Contrary to the conclusions of McKay and Verts (1978*b*), *S. nuttallii* used forms much more frequently (78 [12.4 percent] of 630 cottontails observed during February-August 1981) than crevices and fissures in rock outcrops (four [0.6 percent] of 630 cottontails). However, numerous cottontail tracks were observed to lead to and from openings in rock outcrops during cruises conducted when snow covered the ground in winter 1980-1981.

Movements (locomote) from one area to another accounted for the largest proportion of behavioral acts observed but accounted for less time than three other behavioral categories (Table 1). Movements tended to be of relatively short duration ($\bar{X}$ = 31 s). Tree climbing accounted for the next greatest proportion of time cottontails were in view (Table 1), but was observed only during July and August. Grooming, interspecific interactions, and transitional acts accounted for the remainder of time that *S. nuttallii* engaged in nonsocial behavior (Table 1).

Social interactions accounted for only 7.3 percent of the total time that cottontails were in view (Table 1), and reproductive interactions accounted for 94.6 percent of the time spent in social interactions. Following of females by males at distances of ≤ 2 m and passive attendance of stationary females by males accounted for 75.3 percent of reproductive interactions observed and for 87.4 percent of the time that *S. nuttallii* engaged in reproductive interactions. Male-male interactions accounted for 5.2 percent of reproductive interactions and 3.8 percent of time spent in reproductive interactions. However, no physical contact between males was observed. Although no copulations, attempted mounts by males, or presentations by females were observed, on one occasion (2.6 percent of reproductive interactions, 1.5 percent of time spent in reproductive interactions) the entire "face-off," "male-dash," "jump-sequence," and "reproductive-chase" repertoire that usually is a prelude to mating in *S. floridanus* and *S. aquaticus* (Marsden and Holler 1964) was observed. Presumably, most reproductive interactions occur during the hours of darkness.

Nonreproductive interactions (9.4 percent of social interactions, 5.4 percent of time spent in

social interactions) consisted of a juvenile approaching and investigating an adult female that was feeding and three instances of adult females chasing juveniles that approached them. No physical contact was observed.

Daily Activity

Nuttall's cottontails exhibited a bimodal pattern of daytime behavior with peaks in the second hour after sunrise and the hour before sunset (Table 2). As overall activity increased from the hour before sunrise to 2 hr after sunrise cottontails spent a greater proportion of time feeding (Table 2); in the evening the proportion of time spent feeding tended to increase as overall activity declined in the hour after sunset (Table 2). The proportion of time spent moving and grooming increased as overall activity declined in the morning, likely in response to cottontails seeking daytime retreats and settling in for the midday rest period; both activities increased in the 2 hr before sunset (Table 2). Social interactions tended to be greatest during hours that overall activity was greatest (Table 2).

Seasonal Activity

Among adults, activity levels of the two sexes were similar during March-June, but during July and August, adult male cottontails were not observed from the elevated stand, and were trapped or observed during cruises only about one-third as often as adult females (Table 3). The former period corresponds approximately to the last three-fourths of the breeding season (Powers and Verts 1971). Among juveniles, all indices indicated that activity increased from their first appearance in April through July, followed by a decline in August. An increase in density as each litter-group (Powers and Verts 1971) became observable about 1 month after birth likely was responsible for the observed increase rather than an increase in activity by individuals. The decline in observed activity of juveniles in August likely was a result of a decline in density related to mortality that commonly occurs among juveniles during the summer drought (Verts *et al.* 1984).

Environmental Influences

No single environmental factor or group of factors emerged as a significant determinant of activity levels in Nuttall's cottontail. Many activity-environmental relationships analyzed (Table 4) were not significantly correlated ($P > 0.05$); those correlated significantly ($P \leq 0.05$) usually had low coefficients of correlation (r). Furthermore, relationships with moderate r values usually could be

TABLE 2. Proportion of total activity[a] of Nuttall's cottontails observed in relation to sunrise and sunset by behavioral category on the Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

	Observation Time[b]		Proportion Total Activity[a]	Activity Category							
Interval[c]	(hr)	(%)	(%)	Feed	Rest	Locomote	Groom	Tree-climb	Inter-specific Inter-actions	Transi-tional Acts	Social Inter-actions
SR-1hr to SR	17.6	5.0	3.4	65.0	29.1	5.8				0.1	
SR to SR +1hr	53.9	15.3	20.4	56.4	18.1	6.2	1.1	13.5	<0.1	<0.1	4.8
SR+1hr to SR+2hr	51.7	14.7	27.2	61.3	16.4	7.4	1.8	0.5	<0.1	<0.1	12.6
SR+2hr to SR+3hr	23.6	6.7	7.0	57.0	14.3	14.1	5.3		1.0	0.1	8.3
SR+3hr to SR+4hr	8.1	2.3	2.2	9.4	63.5	17.2	4.7		0.2	<0.1	0.2
SR+4hr to SR+8hr	16.5	4.7	0.6	T[d]		T[d]					
SS−8hr to SS−2hr	27.8	7.9	0.2		T[d]	T[d]				T[d]	
SS−2hr to SS−1hr	40.1	11.4	4.9	55.5	34.3	9.4	0.6				0.1
SS−1hr to SS	54.9	15.6	22.7	51.9	34.6	3.1	1.5		0.5	<0.1	8.3
SS to SS+1hr	33.1	9.4	11.4	77.3	16.0	2.3	0.2			0.1	4.1

[a]Activity = number cottontails in view X time cottontails in view.

[b]Excludes observation time at other than intervals listed; thus, the 327.3 hr listed constitutes only 93.0 percent of the total 352 hr of observations.

[c]SR = sunrise; SS = sunset.

[d]Value omitted because total time cottontails in view in interval <1.0 percent of total.

TABLE 3. Number of marked cottontails in each sex and age class sighted per unit effort during cruises and number captured per unit effort each month on the Terrebonne Study Area, Deschutes County, Oregon, March-August, 1981.

Method of Observation, Effort, and Sex and Age Class of Cottontail	Month					
	March	April	May	June	July	August
Cruises in Area of Intensive Study						
Observation Time (hr)	17.1	9.3	13.9	11.4	18.1	15.7
Number Sighted/10 hr						
Adult Males	3.5	13.9	8.6	3.5		
Adult Females	5.2	12.9	18.7	14.9	12.7	9.6
Juveniles		4.4	6.5	8.8	13.8	11.5
Cruises over Entire Study Area						
Observation Time (hr)		48.6	44.7	33.4	59.0	97.0
Number Sighted/10 hr						
Adult Males		2.5	1.8	0.3	0.7	0.8
Adult Females		3.1	3.1	1.8	2.4	2.5
Juveniles			3.6	2.7	4.1	7.1
Live Trapping on Entire Area						
Number Trap-Nights		1,053	1,053	702	1,434	3,510
Number Captured/100 Trap-Nights						
Adult Males		2.1	0.9	0.3	0.2	0.0
Adult Females		0.7	0.8	0.6	0.4	0.1
Juvenile Males		0.2	0.4	0.9	1.0	0.2
Juvenile Females		0.3	0.4	0.9	0.7	

[a] < 0.1

explained in terms of phenomena other than those of the physical environment. For example, significant positive relationships between number of juvenile cottontails observed per hour and day of year, day of 26-day reproductive period, consecutive days without precipitation, and length of the previous night (Table 4) likely were largely a reflection of litter-cohorts being recruited to the population as the season progressed. Also, significant positive correlations between activity of adult cottontails and number of owls (Strigidae) present and time they were present (Table 4) likely is merely a reflection of the correspondence of crepuscular activity of owls and cottontails.

Principal-component analysis performed on nine variables selected because of their moderate r values resulted in the creation of three components that explained 70 percent of the variation in environmental variables. The first of these components was considered representative of seasonal influences (day of year, temperature, consecutive days without precipitation, numbers of avian predators present, length of night, and lunar illumination); the second was considered representative of daily influences (time of day, temperature, and wind speed), and the third representative of astronomical phenomena (length of night and lunar illumination). Multiple regression of the principal components on cottontail activity (number observed/hr) did not explain large proportions of the variation in activity. Although the seasonal component influenced activity of adult males the most, the component explained only 11 percent of the variation in their activity. Similarly, the daily component had the greatest influence on activity of adult females, but only 4 percent of the variation in activity was explained by the component. Juvenile activity was related to the seasonal component ($R^2 = 0.22$) and the astronomical component ($R^2 = 0.35$); again, these latter relationships likely result from the sequential recruitment of litter-groups.

Conclusions

Without doubt, the most spectacular and potentially ecologically significant behavior of Nuttall's cottontail is related to its tree-climbing activities. Occupation of this region by Nuttall's cottontail may be dependent upon at least some individuals climbing trees during the summer drought to acquire water exuded by boughs or concentrated in tips

TABLE 4. Coefficients of multiple correlation for number of Nuttall's cottontails observed per hour and environmental variables, Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Environmental Variable	Sex and Age Class					
	Adult Male	Adult Female	All Adults	Juvenile Male	All Juveniles	All Cottontails
Day of Year	−0.34*	0.04	−0.21*	0.67*	0.61*	0.04
Reproductive Period	−0.32*	0.12	−0.13			0.01
Day of 26-day Reproductive Period	−0.28*	−0.05	−0.22*	0.67*	0.61*	0.06
Time of Day	−0.08	−0.16*	0.08	0.08	0.02	−0.09
Time Relative to Sunrise or Sunset	−0.06	−0.16	0.07	0.09	0.01	−0.08
Owls Observed (*n*/hr)	0.29*	0.01	0.21*	−0.03	−0.04	0.11
Time Owls Present (Morning)	0.29*	0.02	0.18*	−0.14	−0.19*	0.05
Time Owls Present (Evening)	−0.05	−0.04	−0.05	−0.15	−0.18*	−0.11
Hawks Observed (*n*/hr)	0.01	−0.04	−0.03	−0.14	0.08	−0.07
Avian Predators Observed (*n*/hr)	0.23*	−0.01	0.14*	−0.07	−0.01	0.05
Minimum Temperature	−0.25*	−0.19*	−0.31*	0.11	0.01	−0.21*
Maximum Temperature	−0.32*	−0.20*	−0.32*	0.24*	0.01	0.19*
Mean Temperature	−0.29*	−0.20*	−0.33*	0.18*	0.07	−0.21*
Minimum Temperature Previous Day	−0.34*	−0.06	−0.30*	0.38*	0.25*	−0.13
Maximum Temperature Previous Day	−0.32*	−0.03	−0.25*	0.43*	0.34*	0.06
Consecutive Days With Precipitation	0.10	−0.03	0.06	0.26*	−0.12	<0.01
Consecutive Days Without Precipitation	−0.23*	−0.05	−0.18*	0.66*	0.57*	0.09
Minimum Cloud Cover	0.05	−0.09	−0.05	−0.23*	−0.26*	−0.16*
Maximum Cloud Cover	0.17*	−0.08	0.03	−0.13	−0.18	−0.08
Mean Cloud Cover	0.12	−0.09	−0.01	−0.18*	−0.22*	−0.12
Minimum Wind Speed	−0.09	−0.21*	−0.17*	−0.09	−0.12	−0.21*
Maximum Wind Speed	−0.06	−0.18*	−0.14*	0.07	0.01	−0.16*
Mean Wind Speed	−0.07	−0.20*	−0.16*	0.04	−0.02	−0.18*
Length of Previous Night	0.21*	−0.15*	0.04	0.69*	0.61*	0.03
Duration of Lunar Illumination	0.16*	−0.06	0.07	0.29*	0.27*	0.06
Fraction of Moon Illuminated	0.01	−0.04	−0.04	0.18*	0.18*	−0.02
Time Lunar Illumination Commenced	0.22*	0.01	0.14*	0.17	0.17	0.14*
Time Lunar Illumination Ended	−0.08	0.01	−0.03	0.14	0.09	<−0.01
Phase of Moon	−0.17*	−0.10	−0.18*	−0.03	−0.01	−0.14*
Duration of Lunar Illumination X Fraction of Moon Illuminated	0.05	−0.08	−0.03	0.24*	0.21*	−0.04

*$P < 0.05$.

of boughs of juniper trees (Verts *et al.* 1984). However, the low rate of social interactions during daylight hours may have a role similar to tree climbing in the same ecological relationship: conservation of water may be as critical as acquisition of water for survival of *S. nuttallii* in the intense rain shadow of the Cascade Mountains at the western periphery of its geographic range.

Among leporids, Nuttall's cottontail is at or near the base of the cline in sociality that extends from the warren-inhabiting European rabbit (*Oryctolagus cuniculus;* Mykytowycz 1968), to the swamp rabbit that displays some of the strong social characteristics of the European rabbit, thence to the solitary eastern cottontail that interacts socially only during the reproductive season (Marsden and Holler 1964). In our study, adult Nuttall's cottontails also interacted socially only during the reproductive season. Orr (1940) claimed that *S. nuttallii* is more solitary than other members of the genus. The solitary life-style may be a factor in the relatively uniform dispersion of *S. nuttallii* (McKay and Verts 1978*b*) which in turn may reduce

intraspecific competition and facilitate optimum-forage (moisture) availability at seasons when available moisture is least (Hundertmark 1982) and moisture requirements of lactating females and growing young are greatest (Richards 1979). Presumably restricting energy-demanding reproductive interactions (Marsden and Holler 1964, Casteel 1966) to nighttime hours (when humidities are highest) may be another behavioral mechanism by which Nuttall's cottontail conserves moisture.

Nevertheless, no single environmental factor exhibited a dominant influence on activity of Nuttall's cottontail, a result similar to that obtained in studies of activity in arid-land rodents (Blaustein and Fugle 1981, O'Farrell 1974). Results of our study suggest that seasonal and daily activity levels of *S. nuttallii* during daylight hours may be determined by complex interrelationships among reproductive condition, temperature and moisture requirements of the animals, and combinations of environmental constraints to which populations are subjected.

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Are Lakes in the Cascade Mountains Receiving High Ammonium Deposition?

Abstract

Elevated deposition of nitrogen in the western United States is of concern because of the potential to cause either acidification or eutrophication in mountainous areas containing oligotrophic lakes and streams. A survey of snow chemistry by the U.S. Geological Survey reported NH_4^+ concentrations for the Oregon Cascade Mountains up to 10 μeq/L, approximately 5 to 10 fold greater than concentrations reported in several previous investigations and with results of snow cores collected for this study. Inconsistencies in the snow chemistry data collected by the USGS suggest possible errors in the reported NH_4^+ concentrations. USGS reported NH_4^+ concentrations also are inconsistent with information on regional sources of NH_4^+ and transport and transformation of air pollutants. Actual concentrations of NH_4^+ in snow along the Oregon Cascades appear to be near background levels (~ 1 μeq/L) expected for remote areas in northern temperate climates. The highest concentrations of NH_4^+ in the western mountains are found in the Sierra Nevada of California located downwind of major agricultural sources.

Introduction

Most information regarding deposition chemistry in the western United States (NADP/NTN 1984-1990; Young *et al.* 1988) indicates low rates of acidic deposition, and results from paleolimnological (Charles *et al.* 1989) and lake chemistry studies (Landers *et al.* 1987; Charles 1991; Baker *et al.* 1990) suggests that little, if any, chronic acidification has occurred in the West. Nevertheless, the low base cation concentrations in many of these lakes may cause them to be more susceptible to acidic inputs than acidified lakes in the eastern United States, such as in Adirondack Park, New York (Eilers *et al.* 1989). Because of the dilute nature of lakes in the West, moderate concentrations of atmospheric contaminants, which would not be cause for concern for lakes in the eastern United States, could potentially cause water quality problems in dilute alpine and subalpine lakes in the West.

Laird *et al.* (1986a,b) reported concentrations of major ions and selected metals for alpine/subalpine snowpacks extending from the U.S./Canadian border to the southern Sierra Nevada. Generally, they found that anthropogenic sources were relatively insignificant in affecting the concentrations of H^+, SO_4^{2-}, and NO_3^- and other chemical constituents in the snow. One of the most striking patterns observed was the one for NH_4^+; concentrations were low in the northern Washington Cascades, but increased abruptly in southern Washington, remained high through the Oregon Cascades, and then decreased again in the Sierra Nevada (Figure 1a). Laird *et al.* (1986a) attributed this pattern to removal of NH_4^+ from snowfall in Washington and California caused by reaction with SO_2 aerosols and consequent formation of ammonium bisulfate and ammonium sulfate. The SO_2 presumably was derived from emissions near Puget Sound in Washington and urban areas in California. They assumed that the higher NH_4^+ concentrations ($[NH_4^+]$) reported for the Oregon and California Cascades (including the southern Washington Cascades) were natural. This manuscript explores alternative explanations to the high $[NH_4^+]$ concentrations reported by Laird *et al.* (1986a,b) in the snowpack of the Cascade Mountains.

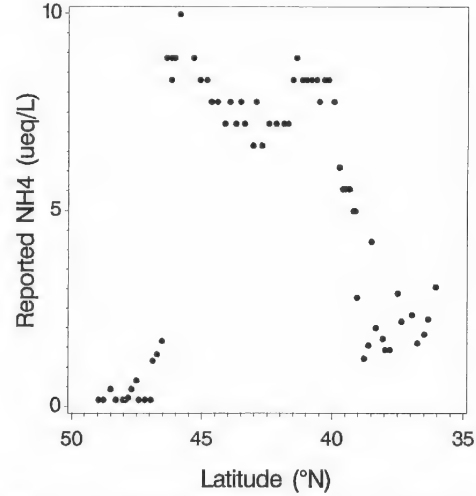

Figure 1a. NH_4^+ concentrations in snow along a transect located on the crest of the Cascade-Sierra Nevada Mountains (derived from Laird *et al.* [1986b]).

One alternate interpretation is that $[NH_4^+]$ are at natural levels for the northern Washington Cascades, implying that $[NH_4^+]$ in the southern Washington, Oregon and California Cascades either are elevated above background levels or are incorrect. Elevated nitrogen deposition has important implications for lakes in the Cascades because transient or long-term nitrogen limitation is increasingly recognized as an important feature of oligotrophic lakes in the West (Morris and Lewis 1988). Other examples of nitrogen-limited lakes reported in the West include Crater Lake (Larson 1988), Lake Tahoe (Goldman 1981), and Castle Lake (Axler *et al.* 1981).

In addition to serving as a nutrient, NH_4^+ can act as an acidifying agent through biological assimilation of NH_3 leaving up to one or two moles of H^+ for each mole of NH_4^+ (Schindler *et al.* 1985; Asman and Diederen 1987; Schuurkes and Mosello 1988). Lakes in the Cascades are considered highly susceptible to acidic deposition because they have extremely low base cation concentrations (some lakes have base cation concentrations <20 μeq/L) and alkalinity values that are as low as 10 μeq/L in the fall (Landers *et al.* 1987) and even lower in the spring (Eilers *et al.* 1990). Thus, the potential for acidification of these lakes by NH_4^+ is particularly high. The average $[NH_4^+]$ reported by Laird *et al.* (1986b) for the Oregon Cascades is about 8 μeq/L, equaling the combined concentrations of all other measured cations in the snow.

Here I re-examine information on deposition for the Cascade-Sierra Nevada ranges, with particular emphasis on NH_4^+ deposition data for the Cascades as reported by Laird *et al.* (1986a,b). This analysis is accomplished by: 1) examining the internal consistency in the Laird *et al.* data; 2) comparing their data with results from other studies; and 3) evaluating potential sources of NH_4^+.

Methods

The snow chemistry data reported in Laird *et al.* (1986a) were obtained from Laird *et al.* (1986b) and scanned directly into a computer file to avoid data entry errors. Concentrations of the various analytes were converted into equivalent units. The equivalent concentrations for individual ions and sums of anions and cations were plotted against one another and against latitude. The literature was reviewed for other relevant studies regarding deposition chemistry in the Cascade Mountains.

A further check on snow chemistry was made by collecting multiple snow cores at two sites in the Oregon Cascades. In April, 1989, I collected snow cores at Mt. Hood (elevation 1770 m) in the northern Oregon Cascades and near Willamette Pass (elevation 1680 m) in the central Oregon Cascades during the period of near-maximum snow accumulation. The cores were collected using a standard Soil Conservation Service stainless-steel corer identical to that used by the U.S. Geological Survey (USGS). The cores were kept frozen, and then melted and screened to remove particulates before shipment, and maintained near 4 to 9°C during transit to the laboratory. The samples were analyzed well within the holding times specified for the methods by Environmental Science and Engineering (ESE) chemists; anions were analyzed using ion chromatography (EPA Method 300.6); cations were analyzed using ICAP (EPA Method 200.7). Ammonium was measured with the automated phenate method (EPA Method 350.1) and pH and conductivity were measured using protocols specified for precipitation samples by the Illinois State Water Survey (Methods 150.6 and 120.6 respectively). ESE was selected to analyze the samples, in part, because they have considerable experience with analysis of precipitation samples for the Florida Acid Deposition Network and as contract laboratory for the National Dry Deposition Network. USGS chemists also analyzed several replicate samples from these recent snow cores.

Results and Discussion

This re-examination of snow chemistry in the Cascade Mountains is divided into (1) an analysis of the internal consistency of the Laird *et al.* data, (2) a comparison of the Laird *et al.* data with other measurements of deposition chemistry in the region, (3) an assessment of natural and anthropogenic sources of nitrogen emissions, and (4) a brief examination of processes affecting atmospheric transport and transformation of ammonium in the atmosphere.

Internal Consistency of Laird *et al.* Data

The quality of data can be evaluated in terms of precision (using replicate [i.e., split] samples), bias (using audit samples or comparison with standards), and detection limit (using blanks or a series of samples with incrementally lower concentrations). Laird *et al.* (1986a) reported a precision

of 0.008 mg/L (0.44 μeq/L) for NH_4^+ (as NH_4^+) for split samples and 0.003 mg/L (0.17 μeq/L) for duplicate snow cores. The detection limit for the NH_4^+ analytical method was 0.003 mg/L. Both the analytical and field precision are indicative of high quality data. Samples from the USGS snow study were analyzed in random order with respect to their position in the transect, which should have minimized problems associated with spatially-related bias. No audit samples or standard reference material results were reported for NH_4^+ and no information was presented regarding analytical bias.

The analytical accuracy of the results was evaluated by computing ion balances for the individual snow samples; the sum of anions was computed using Cl^- values corrected for transcription errors in the reported data (H. Taylor, U.S. Geological Survey, Denver, 1988, personal communication). The results show most samples with high cation excess (Figure 1b); however, cation-anion imbalance can also result from unmeasured ions not included in the summations. In surface waters, it is common to observe an anion deficit caused by lack of a direct measure of organic anions (e.g., Linthurst *et al.* 1986). In the Laird *et al.* data, neither organic anions or bicarbonate are included in the anion sum. Bicarbonate is an important anion in precipitation occurring in arid regions in the western United States where entrained soil particles can raise the pH to 6.0 or greater (NADP/NTN 1984-1990). In the Pacific Northwest, however, pH values are generally much lower; all pH values reported by Laird *et al.* were between 5.11 and 5.88 (median = 5.54). Bicarbonate concentrations, estimated using simplifying assumptions of Henry's Law (Butler 1982) could potentially equal about 3 μeq/L for samples with high pH values (median $[HCO_3^-] \sim 1.7$ μeq/L). There appears to be little association, however, between estimated HCO_3^- and reported NH_4^+ ($r = +0.15$) as might be expected if HCO_3^- was the principal unmeasured anion. Estimated $[HCO_3^-]$ show a pattern of increased values in the middle of the transect, but the concentrations are far lower than required to balance the $[NH_4^+]$ (Figure 1c).

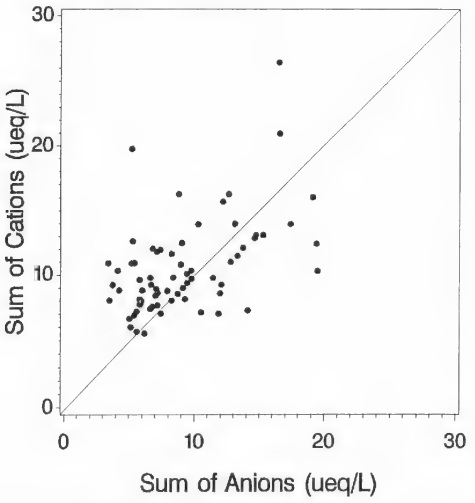

Figure 1b. Sum of measured cations (Ca^{2+}, Mg^{2+}, Na^+, K^+, H^+, NH_4^+) versus the sum of measured anions (SO_4^{2-}, NO_3^-, Cl^-, F^-) for the original data reported by Laird *et al.* (1986b) using observations with Cl^- values corrected for transcription errors. One observation >30 μeq/L omitted.

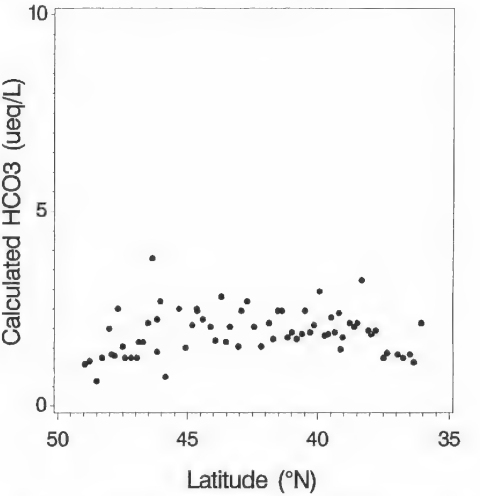

Figure 1c. Bicarbonate, estimated from pH reported by Laird *et al.* (1986b), plotted against latitude.

Organic anions can also be important constituents in precipitation samples. Keene and Galloway (1984) reported that concentrations of acetic and formic acids accounted for 16%, by volume, of free acidity in precipitation samples from Virginia; they estimated that organic acids in NADP/NTN samples, presently unmeasured, may represent 18-35% of the free acidity. Sickman and Melack (1989) reported concentrations of low-molecular weight organic anions (formate, acetate) ranging from 2.8 to 5.3 μeq/L for snow pit samples in

the southern Sierra Nevada; acetate concentrations exceeded the concentrations of other measured anions. The cation-anion difference plotted against reported dissolved organic carbon (DOC) for the Laird *et al.* data show a significant positive relationship ($r = +0.33$, $P < 0.001$), but the relationship accounts for only 11% of the variance in the ion imbalance. An examination of organic anion concentrations computed from pH and DOC (Oliver *et al.* 1983) in Figure 1e shows little correspondence to the distribution of $[NH_4^+]$ along the study transect shown in Figure 1a. Combining organic anions (estimated from DOC and pH) with the estimated HCO_3^-, however, the ion imbalance observed in Figure 1b is reduced (Figure 1d). A similar effect can be achieved by scoring all observations with reported NH_4^+ exceeding 1 μeq/L from sites north of latitude 39° to 1 μeq/L, a concentration consistent with other measurements of NH_4^+ for the region (Figure 1f). The ion imbalance in the Laird *et al.* data is not conclusive evidence of an analytical problem. Unmeasured anions, particularly organic acids, could account for much of the ion imbalance. However, the organic anions, as estimated from DOC, show little association with NH_4^+ or with latitude.

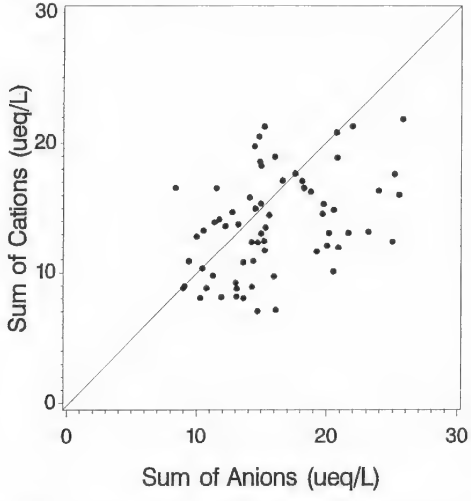

Figure 1d. Sum of measured cations versus the sum of measured anions from the original data reported by Laird *et al.* (1986b). The anion sum has been adjusted by using Cl^- values corrected for transcription errors and by adding estimates for bicarbonate and organic anions. Two observations >30 μeq/L omitted.

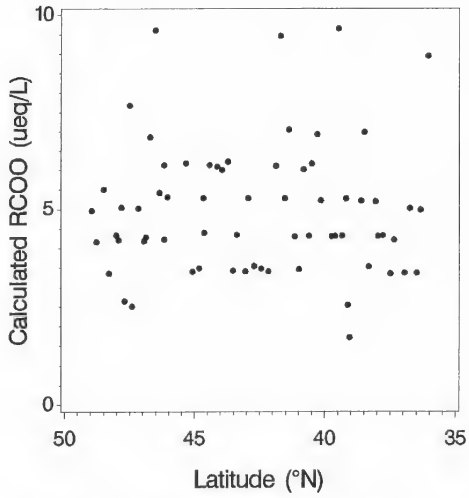

Figure 1e. An estimate of organic anions ($RCOO^-$; Oliver *et al.* 1983) computed from the measurements of DOC and pH by Laird *et al.* (1986b) plotted against latitude. Three observations >10 μeq/L omitted.

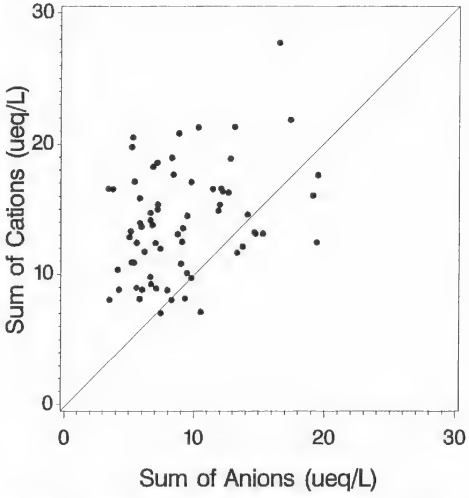

Figure 1f. Sum of measured cations versus the sum of measured anions in the snow data of Laird *et al.* (1986b). Cl^- transcription errors have been corrected and all NH_4^+ concentrations greater than 1 μeq/L for sites north of latitude 39° have been scored to 1.

Also of concern is the internal consistency of the summary statistics for NH_4^+, as presented by Laird *et al.* (1986a, Table VI). They reported median and mean concentrations of 0.01 mg/L

(0.55 μeq/L) and 0.08 mg/L (4.4 μeq/L; n = 70), respectively. I computed a mean $[NH_4^+]$ equal to their reported value, but I computed a median concentration of 0.05 mg/L (2.5 μeq/L), five times the value reported by Laird *et al.* (1986a). The differences are not resolved by treating values reported at detection limit differently (e.g., scoring to zero, one-half of detection limit value, etc.) or by variations in treatment of duplicate samples. This inconsistency could be caused by a transcription error in either the final reported median value or a series of transcription errors in the individual NH_4^+ observations.

Comparison with Other Deposition Data

Another check on the accuracy of data can be made by comparing the Laird *et al.* snow data with information from other sources. Ammonium data, derived from snow sampling conducted at selected sites in the northern Washington Cascades and the southern Sierra Nevada (Sickman and Melack 1989), show close agreement with the data reported by Laird *et al.* (1986b). Sickman and Melack (1989) reported $[NH_4^+]$ in snow (collected during maximum accumulation) ranging from 0.9 to 2.5 μeq/L in 1987 and from 1.8 to 5.2 μeq/L in 1988, at four watersheds in the Sierra Nevada. In comparison, Laird *et al.* (1986b) reported $[NH_4^+]$ ranging from 1.1 to 2.8 μeq/L for the 10 southernmost sites. Similarly, Loranger and Brakke (1988) reported $[NH_4^+] < 1$ μeq/L, in agreement with those of the 10 northernmost sites from Laird *et al.* Duncan *et al.* (1989) reported volume-weighted mean $[NH_4^+]$ in bulk snow samples collected at two locations in the central Washington Cascades ranging from 0.3 to 1.1 μeq/L at Stevens Pass (elevation 1525 m) and 1.5 to 3.5 μeq/L at Snoqualmie Pass (elevation 1220 m) for 1983-1988, with annual median values of 0.75 and 1.64 μeq/L, respectively. Laird *et al.* (1986b) measured $[NH_4^+]$ ranging from detection limit to 0.66 μeq/L at sites in the vicinity of these two Washington locations.

Some of the earliest snow chemistry measurements in the Oregon Cascades consisted of two snow samples collected adjacent to Waldo Lake (elevation = 1650 m, latitude = 43° 40') by Malueg *et al.* (1972). They reported $[NH_4^+]$ of 1.4 and 0.8 μeq/L for samples collected 1 m below the snow surface in February 1969 and 1970, respectively. Recent snow chemistry data in the Oregon Cascades are also available from bulk deposition data collected at Crater Lake and from two snow cores collected north of Crater Lake. The weekly bulk deposition data collected at Crater Lake (site located near the park headquarters on the southwest rim of the caldera, elevation 2150 m), for the period November through March 1988 show $[NH_4^+]$ in filtered samples of about 1.2 μeq/L on a volume-weighted basis (Reilly 1989). In contrast, Laird *et al.* (1986b) reported $[NH_4^+]$ at site 37 near Crater Lake of 7.8 μeq/L.

I also collected snow core samples at two sites adjacent to sites sampled by Laird *et al.* (1986b). Laird *et al.* (1986b) reported $[NH_4^+]$ concentrations of 8.3 μeq/L and 7.8 μeq/L, for sites near Mt. Hood (site 23) and Willamette Pass (site 33), respectively, whereas I found average concentrations of 1.7μeq/L and < 0.7 μeq/L for snow cores from the same locales (Table 1). The split samples of these recent cores showed close agreement between NH_4^+ measured at a private laboratory (ESE) and USGS. Examination of other ions in the snow samples shows that most of these recent samples also exhibit an apparent anion deficit (Table 1). Hydrogen and bicarbonate ions account for about 1 to 5 μeq/L in these samples, but do little to alter the anion deficit. It is likely that the majority of the anion deficit in these recent snow core samples is attributed to unmeasured organic anions.

Data from NADP/NTN (1984-1990) have been used extensively to characterize deposition chemistry in the United States. NADP/NTN maintains several sites adjacent to or on the western slopes of the Cascade-Sierra Nevada ranges (the number of operating sites varies among years). NADP/NTN reports moderately high $[NH_4^+]$ for some of the sites in the central and southern Sierra Nevada (Table 2), which is consistent with the high proportion of agricultural land use west of the Sierra Nevada. The NADP/NTN data also show low $[NH_4^+]$ for sites in western Oregon and Washington. Annual variability of NH_4^+ at the sites receiving low ammonium deposition was about 1 μeq/L. Variability of NH_4^+ for sites in the West were among the lowest reported in the United States (Knapp *et al.* 1988), suggesting that annual variation cannot explain the deviations between NH_4^+ data reported by Laird *et al.* (1986b) and other investigations.

Two potential problems arise when comparing NADP/NTN data with the Laird *et al.* data. As noted earlier, NADP/NTN deposition collectors in

TABLE 1. Analytical results of snow core, surface snow, and blank samples collected in the Oregon Cascades, April 1989. All analyses were completed by ESE[a] with the exception of the split samples analyzed for NH_4^+ by USGS[b]. Units for all ions are in μeq/L.

Site	Sample Type	pH	Conductivity (μS)	NH_4^+ ESE[a]	NH_4^+ USGS[b]	Ca^{2+}	Mg^{2+}	Na^+	NO_3^-	Cl^-	SO_4^{2-}
Mt. Hood[c]	Core	5.89	3.4	1.9	–	6.7	1.2	3.5	0.3	8.9	4.0
	Core	5.69	3.6	1.5	–	5.6	2.2	7.2	0.3	8.1	4.0
	Surface	5.33	3.4	2.3	2.2	3.0	1.6	3.3	0.5	3.9	5.3
	Blank	5.54	1.5	<0.7	0.2	0.2	0.6	<0.5	<0.1	<0.6	<0.8
Willamette Pass[d]	Core	5.51	2.7	<0.7	–	4.9	1.2	1.7	0.2	1.8	1.2
	Core	5.55	2.6	<0.7	–	4.5	1.3	1.9	0.2	2.6	1.2
	Core	–	–	–	0.9	–	–	–	–	–	–
	Blank	5.54	1.7	<0.7	–	0.3	0.7	<0.5	<0.1	<0.6	<0.8

[a]Environmental Science and Engineering, Inc., Gainesville, FL.

[b]U.S. Geological Survey, Arvada, Colorado. Results represent the mean of five replicate analyses.

[c]Samples collected on April 4 west of Timberline Lodge, latitude 45° 19' 50", longitude 121° 43' 01". Snow depth was approximately 5 m, but the corer only penetrated to about 2.5 m. ESE laboratory codes are ARLP* 15 through 18; field codes are T-1 through T-4.

[d]Samples collected on April 2 west of Willamette Pass Ski Area, latitude 43° 35' 50", longitude 122° 02' 23". Snow depth was about 3 m. All cores penetrated to the soil layer. ESE laboratory codes are ARLP* 11, 12, and 14; field codes are W-1, 2, 3, and 5.

TABLE 2. Mean annual (and winter quarter [Dec-Feb]) volume-weighted $[NH_4^+]$ for NADP/NTN sites located west of and adjacent to the Cascade-Sierra Nevada ranges (Source: NADP/NTN 1984-1990).

Site	Latitude	Elevation (m)	NH_4^+ (μeq/L) 1983	1985	1986	1987	1988	1989
Washington								
Cascades National Park	48° 32'	120	–	–	1.1	1.1	0.6(0.6)	2.2(0.6)
La Grande	46° 50'	607	–	–	1.7	2.8(1.7)	1.1	3.3(0.6)
Oregon								
Bull Run	45° 27'	267	–	2.2(2.2)	1.7	3.3	2.2(1.1)	6.1(1.7)
H. J. Andrews Experimental Forest	44° 12'	436	–	0.6	1.1	1.1(0.6)	0.6(0.6)	1.1(1.1)
California								
Montague	41° 45'	805	–	–	5.0	5.0(3.9)	3.9(2.2)	6.1(6.1)
Yosemite National Park	37° 47'	1408	5.0	–	–	–	–	18.8
Sequoia National Park	36° 34'	1856	7.2	8.3(2.8)	14.4	–(5.5)	–(1.7)	15.5(4.4)

the West are typically located 1000 to 2000 m lower than the alpine and subalpine lakes. Deposition chemistry is expected to change with elevation as a consequence of a variety of processes including differences in dry and occult deposition, increasing distance from emission sources, and changing proportions of rain and snow. However, it is unlikely that sites at lower elevation would exhibit lower $[NH_4^+]$ than high elevation sites in the same vicinity. Blanchard *et al.* (1989), for example, found the $[NH_4^+]$ in deposition increased with decreasing elevation along a transect in southern California (elevation ranged from 140 m to 2800 m). Another possible limitation of the NADP/NTN data for this comparison is the delay in collection and analysis of the precipitation samples from the buckets resulting in possible loss of nitrogen from the samples. It seems reasonable to assume, however, that delays would affect samples from all sites, not just those from selected sites in the transect. Thus, the presence of appreciable concentrations of NH_4^+ from the California NADP/NTN sites

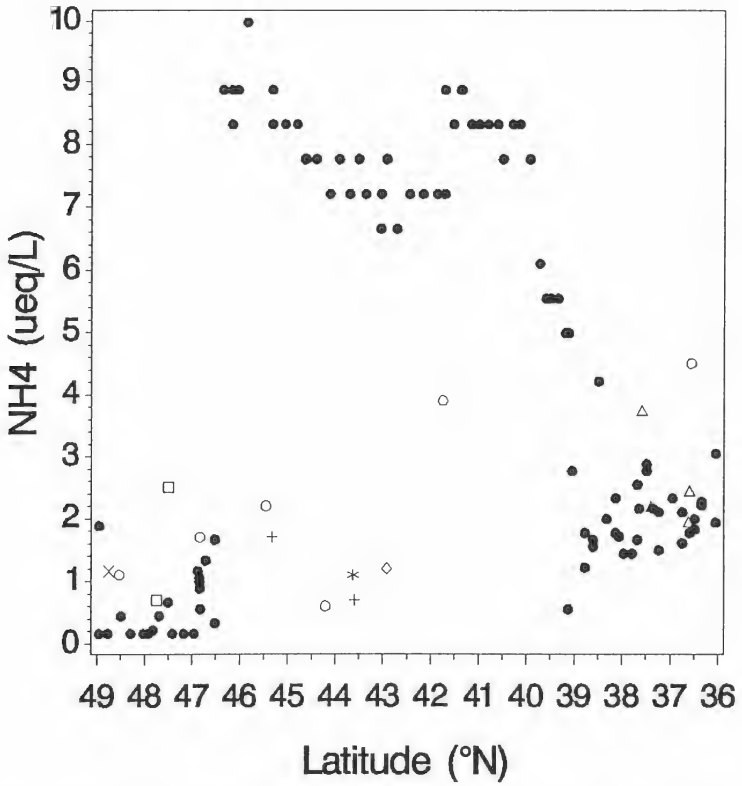

Figure 2. NH_4^+ concentrations in snow reported by Laird *et al.* (1986a,b)(•), compared to precipitation and snow chemistry reported by NADP/NTN (1984-1989) (○); Duncan *et al.* (1989) (□); Loranger and Brakke (1988)(x); Malueg *et al.* (1972) (*); Reilly (1989) (open diamond); Sickman and Melack (1989) (△); and this study (+).

suggests ammonium loss from the wet deposition samples is probably insufficient to explain the discrepancy between the USGS snow core data and the NADP/NTN precipitation data.

Other precipitation data for the West generally show NH_4^+ concentrations that are comparable to concentrations reported by NADP/NTN; concentrations were generally less than 1 μeq/L in western Oregon and slightly greater than 2 μeq/L in western Washington (Junge 1958). Precipitation concentrations on the east side of the Cascades exceeded 20 μeq/L NH_4^+ during the spring and summer, but these sites were located in agricultural areas with alkaline soils where NH_4^+ emissions would be high and retention in the soils would be comparatively low. The data from these recently cited deposition studies, when plotted against the Laird *et al.* data (Figure 2), show a marked deviation beginning near latitude 46° (southern Washington) and extending southward to latitude 39° (northern California).

Sources of NH_4^+

Ammonium is naturally emitted from soils and forest litter during denitrification. The rate of NH_4^+ emission is, in part, a function of the pH of the media. Alkaline conditions favor emission of NH_4^+, whereas NH_4^+ is more highly retained under acidic conditions. Thus, precipitation in areas of the Great Basin and the central United States contain greater [NH_4^+] than areas west of the Cascades (Junge 1963). The Spodosols, Inceptisols, and Ultisols in western Washington and Oregon are relatively low in base saturation and pH and these soils would not be considered major sources of NH_4^+ to the Cascades.

Anthropogenic sources of NH_4^+ can be significant in some areas. For example, feedlots (beef, hogs, poultry) and dairy operations are principal sources of NH_4^+ affecting surface waters in the Netherlands (Schuurkes and Mosello 1988). In the Pacific Coast states, livestock densities were greatest in the Sacramento/San Joaquin Valley of California which may explain, in part, the higher NH_4^+ deposition measured at NADP/NTN sites located east of the valley. Three of the four largest cattle-producing counties in California were located in the San Joaquin Valley upwind of the Sierra Nevada. Livestock densities in California exceeded those in Oregon by a factor of 2 for beef cattle, 5 for dairy cattle, and 14 for poultry; densities for hogs and sheep were comparable (Hornbeck 1983; Jackson 1975). Most livestock operations in California are also located in the central valley upwind of the Sierra Nevada, whereas there is a more uniform distribution of livestock on either side of the Oregon Cascades.

Combustion of vegetation and wood products also can be a significant source of nitrogen emissions. Wood burning for home heating purposes, however, appears to be insignificant relative to the magnitude of the $[NH_4^+]$ differences along the transect. Potassium, often associated with combustion of wood products, showed no concomitant increase with NH_4^+ in the Laird *et al.* data. Furthermore, emissions inventories of NO_x (Wagner *et al.* 1986) are inconsistent with the spatial patterns in NH_4^+ reported by Laird *et al.* (1986a). California ranked 2nd in the United States in NO_x emissions (1.4M tons/yr), compared to only 0.29M ton/yr for Washington (rank 30th) and 0.23M tons for Oregon (rank 37th). There appears to be no major source of NH_4^+ to explain the relatively high concentrations in the Cascades reported by Laird *et al.* (1986a,b).

Transport and Transformation of NH_4^+

The mechanism for supposedly lower $[NH_4^+]$ in Washington and California offered by Laird *et al.* (1986a) is inconsistent with the behavior of $(NH_4)_2SO_4$ particulates. They suggested that SO_2 emissions at the northern and southern ends of the transect oxidized and reacted with ammonia, forming ammonium bisulfate and ammonium sulfate which subsequently deposited before reaching the mountains. However, ammonium sulfate particulates are easily transported. Data from visibility monitoring sites show that ammonium sulfate particulates account for about 20 to 50% of the fine particulate mass in the West (Trijonis *et al.* 1990). The widespread distribution of ammonium sulfate particulates in the United States is evidence of the ease with which $[NH_4^+]$ is transported great distances. Yet visibility along the transect is greatest at the Crater Lake visibility monitoring site with a median visual range of 176 km (Energy and Resource Consultants, Inc. 1988), suggesting that ammonium sulfate particulates and ammonium deposition rates in the Oregon Cascades are very low. Thus, although ammonium sulfate aerosols are formed as a consequence of SO_2 emissions, there is no evidence that this process disproportionately affects the ammonium concentrations in the snow along the transect.

Summary and Conclusions

Laird *et al.* (1986a) speculated that the pattern of NH_4^+ concentrations in snow along the crest of the Cascade-Sierra Nevada was caused by a loss of NH_4^+ at both ends of the transect. Data from areas with low deposition of SO_4^{2-} strongly suggest that $[NH_4^+]$ are naturally low in northern Washington. Rather than being low as a consequence of anthropogenic emissions of SO_2, NH_4^+ deposition in the southern Sierra Nevada appears to be elevated above natural levels (NADP/NTN 1984-1990; Blanchard *et al.* 1989).

Based on a re-examination of these and other data, I conclude that the relatively high $[NH_4^+]$ reported for the Cascades by Laird *et al.* are incorrect and that the highest $[NH_4^+]$ in deposition in this region occurs in the southern Sierra Nevada. The evidence to support this conclusion includes (1) the internal inconsistency of Laird *et al.* data; the ion imbalance is inconclusive evidence of an analytical error, but the lack of agreement in reported and calculated median $[NH_4^+]$ is very suspicious; (2) the inconsistency between Laird *et al.* data and deposition data from several independent sources (Junge 1958; NADP/NTN 1984-1990; Maleug *et al.* 1972; Reilly 1989; this study); USGS reports an average $[NH_4^+]$ of 8 μeq/L for the Oregon Cascades compared to values near 1 μeq/L for other studies; (3) the lack of appreciable sources of natural and anthropogenic emissions of nitrogen in Oregon; livestock densities and fertilizer-intensive crops are substantially lower in Oregon compared to California, which explains

the higher concentrations of NH_4^+ in the Sierra Nevada; and (4) the lack of realistic mechanisms for transporting and transforming nitrogen species; ammonium sulfates are capable of being transported considerable distances, yet ammonium sulfate particulate concentrations are very low in Oregon. Available evidence indicates that $[NH_4^+]$ in snow in the Oregon Cascades are lower than values reported by Laird *et al.* by nearly an order of magnitude and are generally about 1 μeq/L.

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Morphological Differences Between Lynx and Bobcat Skulls

Abstract

This study sought to identify characters of potential value in discriminating between the skulls of the Canada lynx (*Felis lynx*) and bobcat (*Felis rufus*) in British Columbia. Skulls of 32 bobcats and 29 lynxes were examined. Differences were found in the angle of the infraorbital foramen, the size of the postorbital process of the jugal bone, and the number of minor palatine foramina. These, plus previously described differences, were ranked in order of utility for species identification. Separation between the species was greatest for the angle of the infraorbital foramen, height of the postorbital process of the jugal bone, proximity of the major palatine foramen to the orbital rim of the hard palate, and the shape of the choanal border of the palatine. No single character separated the species; however, each specimen could be identified using a combination of three characters. The rank order of discriminatory value of the characters may aid in judging the likelihood of correctly identifying skull fragments.

Introduction

The bobcat and the Canada lynx are sympatric in British Columbia. Methods of distinguishing between each cat species from its bony remains are useful to biologists, wildlife technicians, archaeologists, and forensic investigators. Recognition of intact skulls is not difficult, but identification using bone fragments and damaged skulls is problematic. This study sought to expand the inventory of skull characters that may be of potential value in species identification.

Previous works have identified interspecific differences between lynx and bobcat skulls in the positions of the hypoglossal foramen and the major palatine foramen, shapes of the presphenoid bone, temporal ridge, and choanal border of the palatine, frequency of bregmatic bones, and sizes of the teeth, mandible, zygomatic arch, tympanic bulla, nuchal crest, postorbital process of the frontal bone, and interorbital region (True 1887; Pratt 1942; Glass and Martin 1978; Werdelin 1981; Trail and Tumlison 1984). This report redefines many of these variables as discrete attributes or threshold ratios, describes additional characters, and provides some information regarding constancy within each species.

Methods

The skulls of 32 bobcats and 29 lynxes collected in British Columbia were examined. The bobcat sample contained 17 males, 4 females, and 11 of unknown sex. The lynx sample contained 10 males, 6 females, and 13 of unknown sex. All skulls were from adult animals and are representative of locations scattered over much of the geographic range of each species within the Province. The lynx sample had a mean basal length of 102.7 mm (89.7-109.9), and the bobcat sample had a mean of 104.5 mm (86.6-116.2). Specimens are held by the Cowan Vertebrate Museum, University of British Columbia; the Royal British Columbia Museum; and the Selkirk College Biology Collection.

Bobcat skulls were identified by the presence of both a narrow presphenoid bone and a confluence of the hypoglossal foramen with the posterior lacerate foramen. Lynx skulls were identified by the presence of both an inflated presphenoid bone and separation of the aforementioned foramina (Cowan and Guiguet 1965; Banfield 1974; Trail and Tumlison 1984). Skins were not available for inspection from most specimens.

Each skull was examined with respect to the variables listed in Figure 1 and Table 1. Measurements (to 0.05 mm) were taken using a metric dial calliper.

Results

The robust development of the zygomatic arch of the bobcat skull tilts the infraorbital foramen so that its long cross-sectional axis lies closer to the horizontal than that of a lynx. The long axis of the cross-section of the foramen, when viewed from the front and aligned with a straight edge, intersects the nasal bone. The well developed zygomatic arch also provides greater closure of the orbit in the bobcat, with a jugal postorbital process larger than the space in the rim of the orbit. In most lynxes, this space is larger than the postorbital process of the jugal, and the infraorbital angle does not intersect

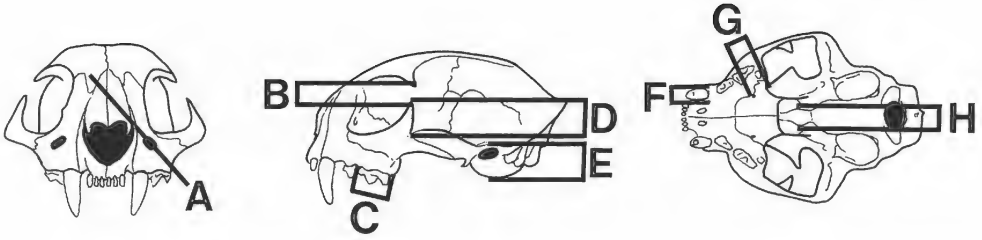

Figure 1. Skull variables: A, angle of infraorbital foramen; B, space in rim of orbit; C, alveolar length of P^4; D, height of postorbital process of jugal; E, depth of tympanic bulla ventral to temporal crest; F, alveolar width of C^1; G, least distance of major palatine foramen from orbital rim of hard palate; H, greatest width of presphenoid bone (irrespective of shape).

TABLE 1. Frequency of occurrence of morphological features in lynx (n = 29) and bobcat skulls (n = 32) listed in order of discriminatory value. (Three damaged skulls could not be completely measured.)

Character State	Lynx	Bobcat
Angle of infraorbital foramen projects dorsal to caudal border of nasals (vs. intersects with nasal bones).	0.97	0
Choanal border semicircular.	1.00	0.03
Height of postorbital process of jugal bone above temporojugal suture < space in orbital rim.	0.96	0.06
Distance between major palatine foramen and orbital rim of hard palate < width of presphenoid bone.	1.00	0.10
Distance between major palatine foramen and orbital rim of hard palate < alveolar width C^1.	1.00	0.19
Distance between major palatine foramen and orbital rim of hard palate < space in rim of orbit.	1.00	0.23
Depth of tympanic bulla ventral to temporal crest < alveolar length P^4.	0.93	0.16
Height of postorbital process of jugal above temporojugal suture < width of presphenoid bone.	0.57	0
No more than one minor palatine foramen.	0.96	0.44

the nasal bones. Minor palatine foramina are limited to a total of one or zero in most lynxes, whereas most bobcats have two or more.

These characters plus others from the literature were ranked in terms of constancy of interspecific differences. The greatest separation between the species involved the angle of the infraorbital foramina, the features of the zygomatic arch described above, the position of the major palatine foramina, and the shape of the choanal border of the palatine (Table 1). In the lynx, the major palatine foramina are close to the orbital rim of the hard palate. This distance is less than the alveolar width of C^1, less than the diameter of the presphenoid bone, and is less than the size of the space in the rim of the orbit. The choanal border of the lynx skull is semicircular, whereas that of the bobcat skull is squared. Other features examined showed less than 80 percent separation. Nevertheless, every lynx skull conformed to a majority of the lynx-typical statements in Table 1 and every bobcat skull conformed to a majority of the bobcat-typical conditions in Table 1. No bobcat skull had more than four lynx-typical character states, and no lynx skull had less than seven (Figure 2). Every

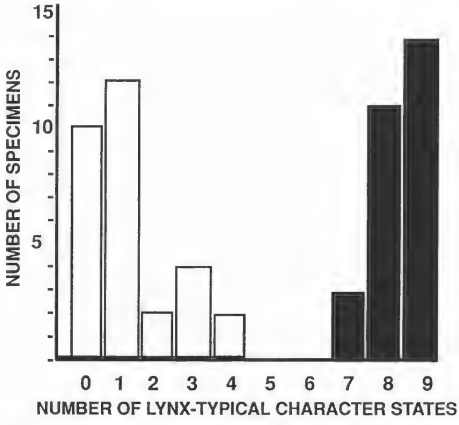

Figure 2. Number of lynx-typical character states found in a sample of 28 complete lynx skulls (black bars) and 30 complete bobcat skulls (open bars).

specimen conformed to a majority of the first three species-typical features in Table 1, and the greatest number of differences was found when using the first seven or more characters.

Discussion

Lynx and bobcat skulls show morphological overlap sufficient to hamper identification based on single characters used in taxonomic keys. The need to employ both the hypoglossal foramen and the shape of the presphenoid bone in identification of skulls was emphasized by Trail and Tumlison (1984). Several additional variables for use in skull identification have been presented here. These are the number of minor palatine foramina, the height of the postorbital process of the jugal, and the angle of the infraorbital foramen. The latter was most frequently different between the species. The rank order of these and other characters presented in Table 1 suggests their potential value in identifying skull fragments.

Anatomical constancy was greater for lynx skulls than for bobcat skulls, but atypical specimens might exist for any character state. For example, Manville (1959) found a bregmatic bone in one of 472 lynx skulls. These findings caution against relying on any single character for field identification of bone fragments or complete skulls.

Although interspecific overlap has been documented with respect to the characters of lynx and bobcat skulls, every skull in this study conformed to a majority of species-typical features. The probability of correct visual identification of lynx and bobcat skull parts is therefore likely to rise dramatically by incrementally considering a combination of characters.

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Book Review

Yellowstone Vegetation. Consequences of Environment and History in a Natural Setting. 1990. Don G. Despain (Roberts Rinehart Publishers, $14.95 paperback).

In this book Dr. Despain shares what he has learned about plant life of Yellowstone during his tenure as a park biologist by describing environmental and resulting vegetational patterns with the hope that readers will understand and appreciate better Yellowstone plant life. Although not specifically stated, this publication seems to be primarily aimed at the more discerning, thoughtful Park visitor rather than the average tourist.

Yellowstone Vegetation starts with a brief introduction of background information about Yellowstone and its vegetation as well as definitions of community taxonomies used. The remainder of the book is divided into three parts. The first two of these parts constitute the majority of the book. Part One contains detailed descriptions of vegetation types in terms of habitat types, thermal communities, and cover types, respectively, while Part Two consists of discussions about origins and causes of the vegetational patterns. Part Three concludes the text with a brief discussion of how such information is used to manage Park vegetation.

This book is well written and for the most part should be easily understood by even the lay reader, although some concepts like "multidimensional environmental space" could be a problem. Discussions of statistics and how environmental conditions obtain are particularly well explained for the "uninitiated," and Chapter 2 (thermal communities) is fascinating reading regardless of background. The author also does an outstanding job portraying the dynamic nature of the Yellowstone vegetational patterns, and readers will certainly agree that any relationships between vegetation and bed rock is ". . . undoubtedly *rooted* [emphasis added] in the soil . . ." (p. 150).

In most cases a general aspect photograph and a closeup of a quadrat-sized area help illustrate descriptions of each habitat type and thermal community type and their properties. A map showing the distribution of habitat types within the Park is also included with each description, and two summary tables facilitate comparisons of forested and grass-shrub habitat types, respectively. Cover types of Yellowstone as perceived by the author are less fully described, and descriptions lack the photographs and maps, although profile silhouettes are provided in the margins. Common names of plants are used in descriptions and throughout the text in general, but the associated scientific names have been listed in Appendix I. The list does not include authors or a source for the nomenclature, nor are significant subspecies indicated (e.g., sagebrushes), but these omissions for the most part should not detract from the usefulness of this appendix.

The one major drawback I see in this book is in the highly subjective approach to community classifications. It would have been helpful to know, for example, why certain plants become "indicator species" in the Yellowstone context. The subjectivity becomes particularly evident when trying to use the Key to Habitat Types (Appendix II). Thus, descriptions such as "the indicated climax," "reproducing successfully," "shrubby aspect," "scarce," and "dominated by" are used throughout the key. The key also violates the need for dichotomies to be mutually inclusive and all inclusive. For example, because a species is "not the indicated climax" does not seem to exclude it from being "present and reproducing." Similarly, another dichotomy has one species at "5 percent or greater cover and reproducing successfully" versus another species that is "dominant and reproducing successfully." Several dichotomies also have a choice between "5 percent or greater cover" and "less than 1 percent cover," which leaves the user in the dark about cases where there is 2, 3, or 4 percent cover. Arbitrary decisions similarly make it difficult to distinguish among some cover types as described.

Finally, the alpine tundra habitat type seems too inclusive. Thus, vegetation on top of Mt. Washburn and similar vegetation might better be interpreted as (subalpine) grassy balds, especially when compared to the more typical tundra of the Absorakas, which has been detailed in numerous reports about the tundra of the Bear Tooth Plateau on the northern end of the Absorakas. There are also some major variations in this tundra recognized by various workers that could be considered different habitat types. This treatment of tundra vegetation is not a serious problem since most

alpine areas in the Park are relatively inaccessible to most visitors.

Despite drawbacks associated with the community taxonomies in this book, the information it contains is a valuable, useful contribution to the literature on Yellowstone National Park. It should be recognized, however, that not everyone who visits Yellowstone will benefit from this information, but any who tour Yellowstone for more than amusement purposes will enjoy and understand better the spectacular vegetation of this national park by perusing Dr. Despain's book beforehand and referring to it on their tour. Groups of academicians, students, or elder-hostel participants touring Yellowstone National Park should derive particular benefit from using this book as a guide. Even those who do not visit Yellowstone might want to read this book for the information it contains about fire management within the Park.

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LETTERS TO THE EDITOR

Snow Chemistry in Cascade-Sierra Ranges

Editor,—This responds to the comments by J. M. Eilers (this issue) relative to the paper by Laird *et al.* 1986, concerning snow chemistry in the Cascade-Sierra ranges of Washington, Oregon and California.

It should be noted that J. M. Eilers has studied the data in the report far more thoroughly than anyone else who has contacted the authors, and his discussion and comments are very much welcomed. His comments are focused primarily on the magnitude of the NH_4 deposition which was an issue of major concern to us during our initial data interpretation. Extensive efforts were made to find a satisfactory explanation for the relatively high levels of NH_4 in the middle part of the sampling transect. There have been numerous exchanges of information with Eilers in an effort to explain the nature of the NH_4 data, particularly, but also to better understand some of the other solutes. Regrettably, we were unable to completely satisfy Eilers' concerns.

The snow chemistry study was funded in 1983 as a reconnaissance effort by the U.S. Geological Survey because at that time there was very little information on the geographical distribution of precipitation chemistry in the Cascades and Sierras and there was concern that melting potentially acidic snows might cause acidification of vulnerable high-mountain lakes. Because of the magnitude of this study, it has not been financially feasible for the USGS to do follow-up investigations.

Snow samples were collected by helicopter and kept frozen until just before analysis. Sampling sites (above 10,000 ft) and dates were carefully chosen to insure that minimal melting of the snowpack had occurred prior to sampling, thereby reducing the probability of solute leaching (a very important consideration) by meltwater. All samples for the determination were analyzed in our Branch of Analytical Services laboratories in random order. The analysts did not know the specific source of the samples. The low NH_4 values at the northern end of the traverse change rapidly but smoothly to higher, relatively uniform values in the middle of the traverse. Given the consistency of the pattern, the probability that such a pattern could occur through chance seems quite small. We have re-examined the methods used for collection-storage, processing and analysis of the snow samples and can find no reason to believe that the NH_4 data are incorrect. Hence, we cannot discard the data just because we may not fully understand them. As indicated in the summary of Laird *et al.* 1986, we would certainly encourage further investigation of the variation in Cascade-Sierra snow chemistry both spatially and temporally. If such a new investigation is made, some caveats are appropriate. The NADP/NTN network attempts to separate dry precipitation from wet precipitation whereas the composite samples in snow cores include both types of precipitation. Therefore, the wet precipitation data alone are not directly comparable to snow cores. Snow cores must be collected before significant leaching of the snow pack occurs in the spring. Note that the snow cores collected by Eilers in the Oregon Cascades were taken in April when there may have been some melting with resultant leaching. Information on the likelihood of such melting would be helpful in deciding whether his samples are truly comparable to those collected by the USGS in 1983. A similar concern applies to subsurface snow sampling which may not represent high dry depositing accumulation; even if the NH_4 concentrations are relatively high in the snowpack, one cannot assume necessarily that NH_4 would be carried into the mountain lakes in that form. Percolation of snowmelt through soil could allow removal of much of the NH_4 from solution because of the great affinity of NH_4, like K, for clay minerals having a 10 Å spacing between layers. Thus, low NH_4 concentrations in snowmelt entering lakes does not prove low NH_4 in the snow from which it came.

There is also potential for biological decomposition of NH_4 in both the NADP/NTN wet deposition collectors and surface waters. The extent of this decomposition is dependent on numerous environmental factors and, therefore, cannot be readily evaluated.

A necessary assumption in proving or disproving the NH_4 levels reported by Laird *et al.* 1986, is that wind patterns, storm paths and pollutant sources in any later period resembled those when the USGS study was done in 1983. For instance, a major copper smelter in Tacoma, Washington, was in operation until 1985. Hence, it will be difficult to ever be absolutely certain that the data reported were or were not representative of existing conditions at that time. However, that simply means that more care must be taken in later studies to avoid factors now known to represent potential problems.

In summary of the above NH_4 discussion, we understand Eilers' skepticism about the NH_4 data and agree that follow-up research is needed to address the question of "high" NH_4 concentrations in snow cores reported by Laird *et al.* 1986. On re-examining the analytical data during discussions with Eilers it became evident that several of the chloride analyses and one of the aluminum analyses were reported by a typographical error to be too high by a factor of 10. Correct values for chloride are listed as follows:

Distance from U.S.-Canadian borders (km)	Concentration Cl (mg/L)
10	0.036
75	0.045
165	0.024
175	0.05
1060	0.10
1090	0.089
1095	0.040
1160	0.096

Literature Cited

Eilers, J. M. 1991. Are lakes in the Cascade Mountains receiving high ammonium deposition? *Northw. Sci.* 65:238-247.

Laird, L. B., H. E. Taylor, V. C. Kennedy. 1986. Snow Chemistry of the Cascade-Sierra Nevada Mountains, *Environ. Sci. Tech.* 20:275-290.

Reanalysis of all the samples for chloride showed no errors other than the typographical. In addition, a typesetting error in the Table VI footnotes should indicate concentration units for aluminum to be micrograms per liter instead of milligrams per liter, and the maximum concentration value for aluminum should be 10 μg/L instead of 100 μg/L.

The first author of the paper by Laird *et al.* 1986, has retired and was not involved in the interaction between Eilers and Taylor and Kennedy.

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